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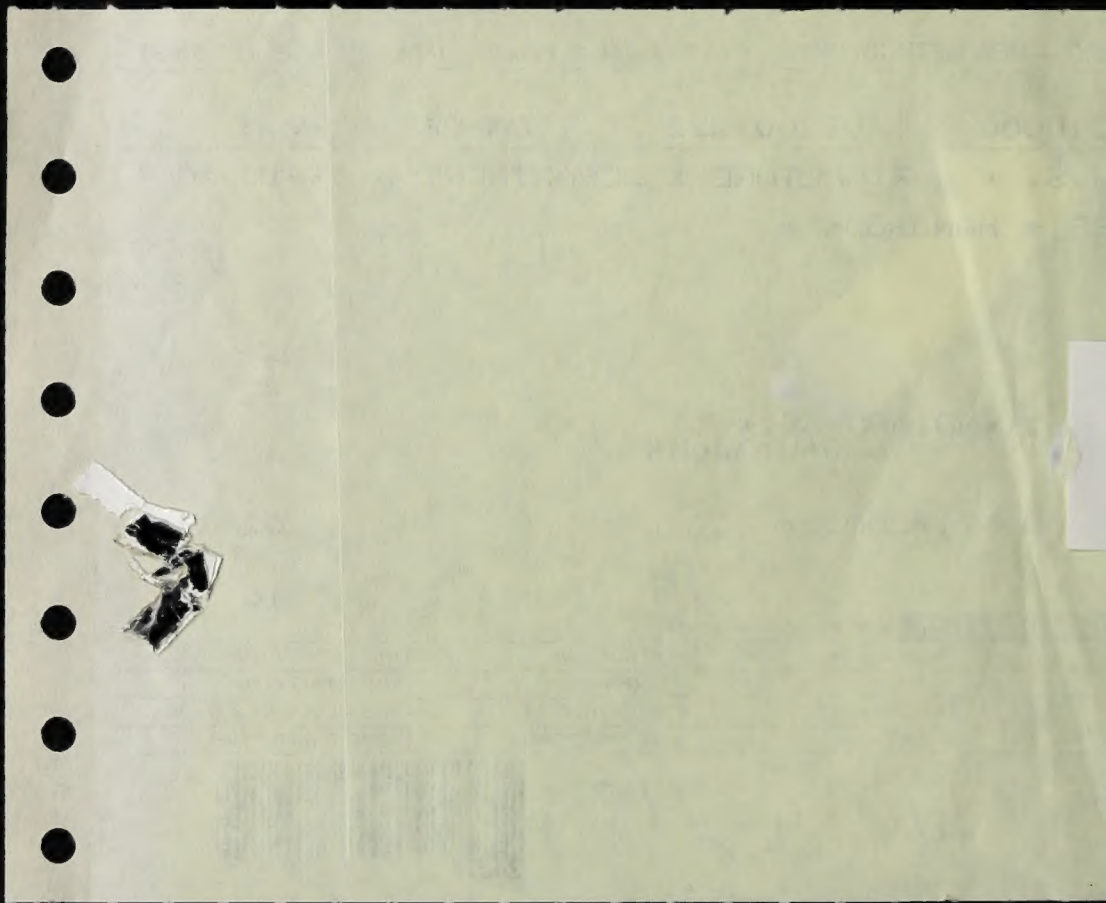
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Forest and Rangeland Birds of the United States

Natural History and Habitat Use

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Agriculture Handbook 688
January 1991

Cover photo: Cedar Waxwings in nest. © R. Reinhold

Using This Book

This book is designed to provide managers with information on the assemblage of bird species that might be expected in forest and rangeland habitats.

In the first section, natural histories are provided for each bird species, including taxonomic information, range and status, habitat descriptions, nest site descriptions, and food habits. These natural histories thus provide a short review of the pertinent information on each species necessary for initial evaluation of management practices for a particular area. The illustrations in the publication are reproduced from *BIRDS OF NORTH AMERICA* by Robbins et al., illustrated by Arthur Singer, © 1983, 1966 Western Publishing Company, Inc., and are used by permission. Nomenclature, distribution, and taxonomic order follow the American Ornithologists' Union (1983).

After the natural history information, a series of matrices list bird species that either breed or winter in 20 forest cover types and 24 rangeland, desert, and other nonforest habitats.

The authors believe this guide can provide a basic source of data to assist land managers in ecologically sound management of resources.

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INTRODUCTION

As North America was settled, many once-abundant birds began to disappear. Some were hunted, but habitat loss or alteration was responsible for most losses. Around the turn of the twentieth century, conservationists began efforts to preserve habitats so that birds, especially plumed wading birds, could survive. Legislation was initiated to assist in the conservation of birds and to manage hunted species. Today, many public and private conservation agencies are involved in managing bird populations and their habitats.

Birds are important components of ecosystems. Birds disseminate seeds and prey upon innumerable insect and vertebrate pests. They are involved in energy transfer as they eat and are eaten. Nutrients are also distributed through the movement of birds. Vultures, crows, ravens, and other scavenging birds are important in natural decomposition cycles. Because birds are not isolated components of our natural systems but integral parts of them, it is vital to understand both their roles and their needs.

Management of birds—whether for human enjoyment, consumptive use, or ecological considerations—requires data on their biology and habitat use, as well as an understanding of community interactions. Wildlife biologists, foresters, rangeland managers, and land-use planners use comprehensive information on the total community—including birds—in habitat management. Information must be available on the species present in the area, their habitat requirements, and how birds will respond to habitat alterations.

The objective of this book is to summarize information on the natural histories and habitat needs of forest and rangeland birds to help managers evaluate the impacts of various actions in different vegetation types. Opportunities can be identified to emphasize birds in management actions and to minimize negative impacts. These data, however, cannot replace the need for on-the-ground evaluations when projects are planned that will alter avian habitats; the natural history and matrix information compiled here must be applied along with local field knowledge.

Distribution of Birds in the United States

There are several broad patterns in the ecological distribution of breeding birds in the United States. There is a generally increasing continuum of breeding bird species from the drier areas of the Southwest and West to the more moist forests of the Northeast (Peterson 1975). Regions dominated by desert vegetation have relatively simple avifaunas that contain a few prominent species. Regions with complex mixed forests contain many rather evenly distributed species, although

much regional variation occurs along this gradient. In the Great Plains, the number of species increases from Texas to the Canadian border (Cook 1969, Peterson 1975). This latitudinal increase may reflect patterns of glaciation or a more heterogeneous landscape on the northern plains, but in general the avian community in grasslands is organized by the most obvious structural feature, grass height (Cody 1968).

Mountainous regions of the United States have relatively diverse avifaunas, largely because their considerable topographic relief compresses several different vegetation zones into a relatively small area, rendering them ecologically diverse (Cook 1969). Closely related habitats, or habitats with similar physical profiles or complexities, exhibit similar bird diversities (Peterson 1975).

Importance of Vegetation Structure

An avian community, as defined here, is an aggregate of species existing together in a definable ecological area that provides the species' requirements. Each species can exist only where its specific requirements are met. Within the general habitat provisions of food, water, and shelter, birds have various specific needs for nest sites, song posts, perch sites, and vegetation structure. Some species have relatively narrow ranges of tolerance for specific factors. A prime example is the Kirtland's warbler, which breeds only in fire-regenerated stands of young jack pine in Michigan's Lower Peninsula. Others, such as the American robin, which breeds throughout North America, have broad ranges of tolerance and so are widely distributed.

Many components of the environment, including vegetation structure, plant species composition, succession, and vegetation layering, affect the distribution of bird species. What is not so obvious is that there are two basic sets of factors, ultimate and proximate, that determine whether a bird can reproduce in a given area. Many of the factors that actually determine reproductive success are not evident at the time the bird arrives or selects its breeding habitat. Keys to these ultimate factors, such as food availability for nestlings, are perceived in advance through proximate factors—aspects of the physical habitat, especially vegetation structure.

Ever since Lack (1933) suggested that birds select breeding habitats by recognizing features they did not immediately require for survival, many studies have been conducted to identify the features or patterns of vegetation structure that bird species were "programmed" to seek. Beecher (1942) expressed a similar idea, and suggested that a bird did not "adapt" to a so-called new habitat but rather chose the habitat because of its programmed ability to recognize potentially satisfactory ultimate factors.

MacArthur and MacArthur (1961) demonstrated that the vertical complexity of forest vegetation (the diversity of vegetation heights and

density of foliage at those heights) affects breeding bird diversity. The relationship of bird species diversity to foliage height diversity has been demonstrated in many forest habitat types (Karr 1968, Karr and Roth 1971, Willson 1974). Foliage height diversity may be an indicator of total foliage volume. The important consideration for managers, however, is that habitat alteration changes the number of bird species and their relative abundances, both of which affect diversity.

Studies of habitat selection and resource partitioning by breeding birds include measurement of many descriptors of stand structure. These stand measurements — canopy height, layering and closure, tree diameter and species composition, understory height and volume, ground cover, etc.—are attempts to identify the proximate factors that birds select when settling on the breeding grounds.

Horizontal diversity or patchiness (the distribution of successional stages, timber size classes, and openings) is also important to breeding bird composition. Roth (1976) demonstrated that the number of bird species increased faster than the degree of species overlap in a series of habitats from grasslands to forests, and that horizontal habitat patchiness was a better predictor of the numbers of bird species than was vertical habitat complexity.

Both the vertical diversity or structure of forest stands and the distribution of stands of different size class or type are typically manipulated in forest management and can be altered as needed to manage the type and availability of bird habitat.

The close relationship between habitat structure and bird species composition is useful for assessing the effects of forest management on breeding birds. For example, as stands of northern hardwoods (sugar maple, American beech, yellow birch) develop after clearcutting, each tree size-class—regeneration, seedlings/saplings, poles, and sawtimber—supports a different breeding bird species composition (DeGraaf 1987). In the Willamette Valley, birds respond to successional patterns as Oregon white oak is replaced by Douglas-fir and finally by true fir and western hemlock. Downy woodpeckers, black-capped chickadees, and white-breasted nuthatches breed in the oaks, while chestnut-backed chickadees, red-breasted nuthatches, and golden-crowned kinglets commonly breed in Douglas-fir stands (Anderson 1970).

Long-term changes in bird populations occur in response to environmental change. As land uses change, or as succession proceeds, bird communities and populations will change. Most habitat management projects are, in effect, attempts to control succession: either setting it back to an earlier stage, arresting it, or allowing it to advance to a desired stage. This process can also be accompanied by short-term changes in which individuals adapt to changing conditions. Outbreaks of some insects, for example, might attract birds to a forest where they normally do not feed, such as the woodpeckers that congregate in areas of mountain pine beetle infestation.

Forest and Rangeland Management

Most forest management activities are not directed primarily at wildlife, but proper planning can help maintain or enhance wildlife habitats while accomplishing other goals. In logging or thinning operations, successional patterns are changed, creating habitat for different species of birds. Clearcutting reduces nesting, shelter, and feeding habitat for forest canopy birds, but the habitats of ground and shrub dwellers will be enhanced. Small rodents will increase in clearcuts and provide a food base for raptors. As the forest regenerates, woodland hawks and owls replace open-country hawks and falcons. Forest canopy birds will replace the ground dwellers.

Even-aged forest management creates forest stands of uniform age or size classes. The forest will have a variety of openings and stands, each with a fairly homogeneous structure, especially in smaller size classes. Thus, over the entire forest, a variety of bird habitats exists.

Uneven-aged forest management produces trees of markedly different ages or sizes in the same stand. Thus, each stand in the forest has a fairly diverse structure, but all stands are fairly similar. The result can be a more diverse bird community in each stand than in any one stand under even-aged management, but it is often less diverse than that in an entire forest under even-aged management, where many successional stages are represented. A northern hardwood forest under even-aged management, for example, supports approximately twice as many breeding bird species as does an extensive uneven-aged forest. The lack of distinct, early successional stages in the uneven-aged northern hardwood forest means that species associated with those habitats—willow flycatchers, cedar waxwings, eastern bluebirds, chestnut-sided and mourning warblers, among others—will not likely be present (DeGraaf 1987).

Deciduous Forests

A striking feature of the bird communities of deciduous forests is the high proportion—up to 75%—of migratory species. Thus the total bird population (the standing crop) is very high in the summer breeding season. Bird communities in coniferous forests are seasonally less variable. In the deciduous forest there is a general pattern of increasing bird density with plant succession (see Shugart et al. 1975 for examples). The general pattern of avian succession is generally acknowledged to be a manifestation of the habitat preferences and ecological requirements of forest birds.

In northern hardwood types, as with other hardwood types, the composition of bird species varies with timber size class, the presence or absence of softwoods in the stand, stand area, the presence of cavity trees, openings, and other within-stand features. In New England,

even-aged sawlog stands have avifaunas very similar to those in uneven-aged stands because the diameter distributions in both are similar; there are essentially no differences in foliage profiles in stands more than 30 years old (Leak 1979, Aber 1979). Thus the breeding bird assemblages in stands beyond the pole stage are similar. On wetter sites, where red spruce comes into mature stands, the softwood component provides habitat for species—especially warblers—that are typically associated with coniferous types.

Oak-pine and oak-hickory types, which together compose most of the inland forests of the United States, support 150 to 200 species of breeding birds. Many are associated with successional stages and wetland and open habitats within these broad types, but their avifaunas are nevertheless quite rich. In oak-hickory types, site quality determines the dominants in mature stands: red, white, and black oak on good sites, post oak and blackjack oak on poor sites, and white and post oak on intermediate sites. Succession in oak-pine and oak-hickory types is similar, except that pine seedlings come in after disturbance during the “brush” stage in oak-pine.

Old-field successional stages are different from those after clear-cutting, especially in the oak-pine type. Old fields produce essentially pure pine stands that persist a long time before oak components appear. After clearcutting, however, all components of the oak-pine types are present throughout stand development (Evans 1978).

Oak-hickory and oak-pine forests, largely due to these differences in their successional patterns, support somewhat different avifaunas. Many species associated with coniferous forests are found in the oak-pine type (see Evans 1978 for review). The larger difference between the two types is the greater value of oak-pine forests to wintering birds because the type is more southern than oak-hickory, and conifers provide additional cover.

In the western United States, aspen stands provide especially rich bird habitats compared to coniferous types. Moist ground surface, high insect populations in the understory, edge effect, and nest hole availability (depending upon woodpecker use and *Fomes* infection) have been identified as factors primarily responsible for the rich avifaunas in these stands (Winternitz 1976).

In both the desert Southwest and the Great Plains, riparian woodlands are essentially deciduous; cottonwoods are important in both regions, although Great Plains riparian woodlands contain more tree species as one moves eastward. These habitats contain bird communities that are as much as seven times as rich as those in the surrounding Plains habitats in general (Tubbs 1980).

In the Southwest, a variety of riparian habitats, each with a more or less unique assemblage of breeding bird species, is extremely important for wintering and migrant species also. Bird density is directly correlated with densities of cottonwoods in these wooded southwestern-riparian zones (Carothers and Johnson 1975).

Coniferous Forests

Approximately 150 bird species are associated with coniferous forests across the United States; the greatest number of species is found in mature forests in the Northeast, and the lowest in young stands in the same region. In other regions of the United States, the number of species is both lower and fairly uniform (Wiens 1975). A general pattern in coniferous forest avifaunas is that they are characterized by a few abundant species. Approximately a quarter of the individuals are of a single dominant species, and one-third to one-half belong to the two most abundant species.

The degree of dominance by a few species decreases with species richness. Several dominant species that occur throughout coniferous forests in the United States include: northern flicker, red-breasted nuthatch, brown creeper, American robin, hermit thrush, golden-crowned kinglet, dark-eyed junco, and chipping sparrow. These species occur in all coniferous regions, and can be considered the group most representative of this vegetation type across the United States (Wiens 1975).

Analyses of the ecological structure of coniferous forest avifaunas—e.g., those of Balda (1969), MacArthur (1958), and Sturman (1968a, 1968b)—have revealed several patterns of habitat utilization. Foliage-gleaning species are the most abundant birds in all North American coniferous forests, while ground-gleaners, bark-gleaners, and aerial feeders are less abundant in decreasing order.

Foliage feeders constitute the greatest proportion in mature northeastern and southeastern coniferous forests. All ground-gleaners are most important in early successional stands, and bark-gleaners and aerial feeders are proportionately more numerous in western coniferous forests.

Among foliage feeders, insectivores predominate in all forest types. Warblers constitute the major component of the breeding avifaunas of the northeastern and southeastern coniferous forests, but their relative densities are lower in the western forests. Both the number of warbler species and their densities are substantially lower in western forests than in eastern North America, and their paucity is not compensated by other foliage-gleaning insectivores. These differences likely reflect differences in prey availability between eastern and western North America (Wiens 1975).

In the longleaf-slash pine forests of the Southeastern and Gulf Coastal Plains, bird species richness can be maintained by retaining dead trees, avoiding extensive monocultures, and controlling—rather than eradicating—understory vegetation (Wood and Niles 1978).

Loblolly-shortleaf pine, a subclimax or developmental stage of oak-hickory, occurs on the Southeastern Coastal Plain and Piedmont—the old Cotton Belt. The red-cockaded woodpecker, the only endangered species closely associated with upland loblolly-shortleaf pine, occurs in clans of 2 to 10 birds in stands at least 80 years old and 35 to 160 acres in size (Meyers and Johnson 1978).

As the loblolly-shortleaf type develops, four stages each have distinct breeding bird assemblages: grassland, shrubland, pine forest, and hardwood forest (Johnston and Odum 1956). Maintaining stands in earlier stages by shorter rotation (about 35 years) is eliminating mature pine and hardwoods. Short rotations eliminate cavity trees, understory vegetation, fruits and mast, and deciduous trees. Many bird species winter in this type. Because species richness declines from early successional stands and begins to increase at about age 35, short rotations adversely affect both breeding and wintering birds (Dickson and Segelquist 1978, Noble and Hamilton 1976, Quay 1947).

The ponderosa pine type, which has the widest distribution of any pine type in North America (Little 1971), occurs in extensive stands in northern California, eastern Oregon, and the intermountain region, and as scattered islands in the Southwest and Rocky Mountains. Because stands range from savannas to mixed pine-broadleaf transition forest to pure ponderosa pine and mixed conifer stands, the type has a wide array of bird species associated with it (Diem and Zeveloff 1980). Where ponderosa pine is an important commercial tree, maintenance of snags and cull trees is important for cavity-nesting birds; a higher proportion of the avifauna is composed of cavity-nesting species in western than in eastern forests.

Where the ponderosa pine type grades into the pinyon-juniper type in the Southwest, the ecotone between the two types contains fewer bird species than does either community alone. In the pinyon-juniper type, the number of breeding species that nest in holes or forage on trunks and branches is directly related to the density of pinyon pines. In winter, bird species richness and density are strongly related to juniper berry production (Balda and Masters 1980).

The Douglas-fir region west of the Cascade Range is intensively managed because timber values are high, especially in old stands. Under natural succession, grass and shrub stages are followed by Douglas-fir, which forms dense, even-aged stands that persist for centuries. Mortality eventually opens the stand, and true climax western hemlock and western redcedar invade and an understory is reestablished. After four to six centuries without disturbance, climax western hemlock replaces Douglas-fir (Franklin and Dyrness 1973).

In intensively managed forests, fire is commonly used for slash removal and seed-bed preparation after harvest cutting. Genetically superior seeds or seedlings are planted, and herbicides, fertilizers, and pest control practices quickly produce even-aged stands of fast-growing Douglas-fir. These trees are harvested at 50 to 150 years of age. This managed succession—shortening the grass-forb and shrub stages and eliminating snags and old-growth forest—directly affects the avifaunal composition. The second (shrub) successional stage, in which approximately 40 percent of the bird species associated with the type nest, is abbreviated.

Fire affects birds indirectly by modifying their habitats. Removal of woody vegetation creates clearings with low vegetation that favors some

birds. Along the border between Arizona and Mexico, for example, open-country birds such as American kestrel, roadrunner, curved-billed thrasher, harlequin quail, and chipping sparrow are most common on the Mexican side where fire control is less stringent. The species most common in Arizona are birds of brushland or dense forest, including the blue-gray gnatcatcher, black-throated gray warbler, Scott's oriole, and rufous-sided towhee (Marshall 1963).

Some species are attracted to new burns, including robins, bluebirds, several sparrows, flickers, several woodpeckers, mourning doves, and pine warblers. Prescribed fire has long been used to produce habitat for bobwhite quail in yellow pine in the Southeast (Stoddard 1963). Breeding-bird density and diversity are slightly higher in burned than in unburned chaparral (Laurence 1966). In lodgepole pine and spruce-fir forests in Yellowstone National Park, numbers of bird species increased for 25 years after fire, then begin to decrease (Taylor 1973).

In the moist, temperate coniferous forests of the Olympic Mountains, large lightning fires are less common than in Wyoming, but a similar avian response occurs over time: more species are unique to the first 20 years after fire than to stages 100 to 300 years later. Habitat for ground- or shrub-foraging species is generally enhanced in the first few years after fire, while habitat for mature-forest birds is decreased. However, during the first 1 to 3 years after fire, the bird community in coniferous forests may be more similar to that in mature forests than to the ground/shrub community (Huff et al. 1984, Bock and Lynch 1970, Bock et al. 1978), with the greatest post-fire changes in the composition of bird species occurring after about 20 years in the western United States.

Kirtland's warbler depends completely on periodic fire to maintain a very specific nesting habitat in young stands of jack pine in Michigan's Lower Peninsula. For detailed information on the effects of fire on bird habitat, see the compilations of Lotan and Brown (1984), Wood (1981), and Wright and Bailey (1982).

Management of cavity trees has become standard silvicultural practice for bird habitat management, but continued availability of contiguous old growth for the northern spotted owl remains a real concern. A detailed review of Douglas-fir management and bird species composition is provided in Meslow and Wright (1975).

Rangeland Habitats

Rangeland avifaunas characteristically have few breeding bird species compared to forests. Approximately 40 species (excluding waterfowl, raptors, and galliforms) occur with moderate frequency across major rangelands of the United States, from the shrub steppes of the Great Basin to the shortgrass, tallgrass, and mixed-grass prairies of the Great Plains (Wiens 1973, 1974). A rather small group of species characterizes each rangeland type; sparrows are present in moderate to high numbers

in all rangeland habitats. There is substantial seasonal and annual variation in total bird density but not in the species composition of breeding birds. Rangeland avifaunas are often dominated by one or a few species, and high dominance is associated with low numbers of breeding species (Wiens and Dyer 1975).

Grazing and grain production are the dominant uses of rangelands. Grazing affects breeding avifaunas in various ways depending upon the intensity and rangeland type. In general, however, where grazing regimes affect vegetative composition only slightly, effects on avifaunal composition are slight. Where intensive grazing produces marked changes in vegetative composition, avifaunal composition changes markedly, usually toward that characteristic of more xeric habitats (Owens and Myres 1973, Wiens 1973). Fencing to control grazing intensity, timing, and location may create a mosaic of range conditions and therefore of bird communities of differing structure and composition.

Type conversion to remove woody vegetation and increase forage production—whether by herbicide, mechanical means, or fire—can be beneficial or detrimental to avian habitats depending upon extent, pattern, successional stages involved, and effects on special habitat needs of certain species. An example of a detrimental effect is the removal of Ashe juniper on the Edwards Plateau of Texas, which is required for nesting by the golden-cheeked warbler, a threatened species. A beneficial effect in fire-treated chaparral is increased species richness, especially where brush “islands” are retained (Bell and Studinski 1972).

The history of western livestock grazing and big game populations and their habitats have been described in detail by Wagner (1978). Generally, bison, bighorn sheep, and cattle feed more heavily on grasses; mule deer and mountain goats on shrubs and trees; and pronghorn and domestic sheep generally feed on forbs. Elk and horse feeding habitats overlap those of all of these other herbivores. Foraging by rodents, rabbits, and hares can profoundly affect rangeland vegetation, especially in desert rangelands (Norris 1950, Rice and Westoby 1978).

The preponderance of evidence indicates that grazing is generally harmful to waterfowl habitat and nesting success (Brown and Johnston 1978, Weller et al. 1958). In the Southwest, heavy grazing has also caused serious declines in populations of lesser prairie-chickens (Brown 1978), greater prairie-chickens, Montezuma quail, California quail (Leopold 1977), and northern bobwhite (Phillips et al. 1964). Intensive grazing is considered the primary factor in the decline of the Columbian sharp-tailed grouse (Miller and Graul 1980). Attwater's prairie-chicken uses grazed pastures more than ungrazed pastures because green herbaceous vegetation is made available by grazing (Kessler and Dodd 1978). In North Dakota, American bitterns, marsh hawks, and short-eared owls nest only in tall, dense ungrazed grasses and legumes (Duebbert and Lokemoen 1977).

The effects of grazing on avian habitats vary from place to place. In areas of higher precipitation, grazing may provide more habitat patchiness and so be generally beneficial to birds. In areas of low precipitation, protection from grazing may be necessary for a species that benefitted from grazing in an area of higher precipitation. Effects of soil, slope, and exposure, as well as amount and seasonal distribution of precipitation may be more important than grazing in affecting the quality of bird habitat (Ryder 1980).

Fire is an important tool in maintaining grasslands. Where fires are suppressed, grasslands may be replaced in successional stages by shrub-dominated communities, thereby providing habitat for different species of birds. For example, control of fire in the upper Midwest has reduced that habitat for sharp-tailed grouse.

Prescribed fire maintains proper cover conditions for both prairie chickens and sharp-tailed grouse in tallgrass prairie and promotes the growth of preferred subclimax foods (Miller 1963).

Creating isolated stands of trees and shrubs often enhances habitat for grassland birds. Thus riparian habitats and shelterbelts receive disproportionate use by birds. These habitats not only have their own bird communities, but are also used by grassland-nesting species as well. Cavity nesters also use riparian habitats extensively. Primary cavity users, those birds that excavate their own nesting and roost cavities, and secondary cavity nesters, which use cavities already present, are common in riparian habitats near grasslands.

Fencerows also provide shelter and nest sites for grassland birds and add to the year-round diversity of bird communities.

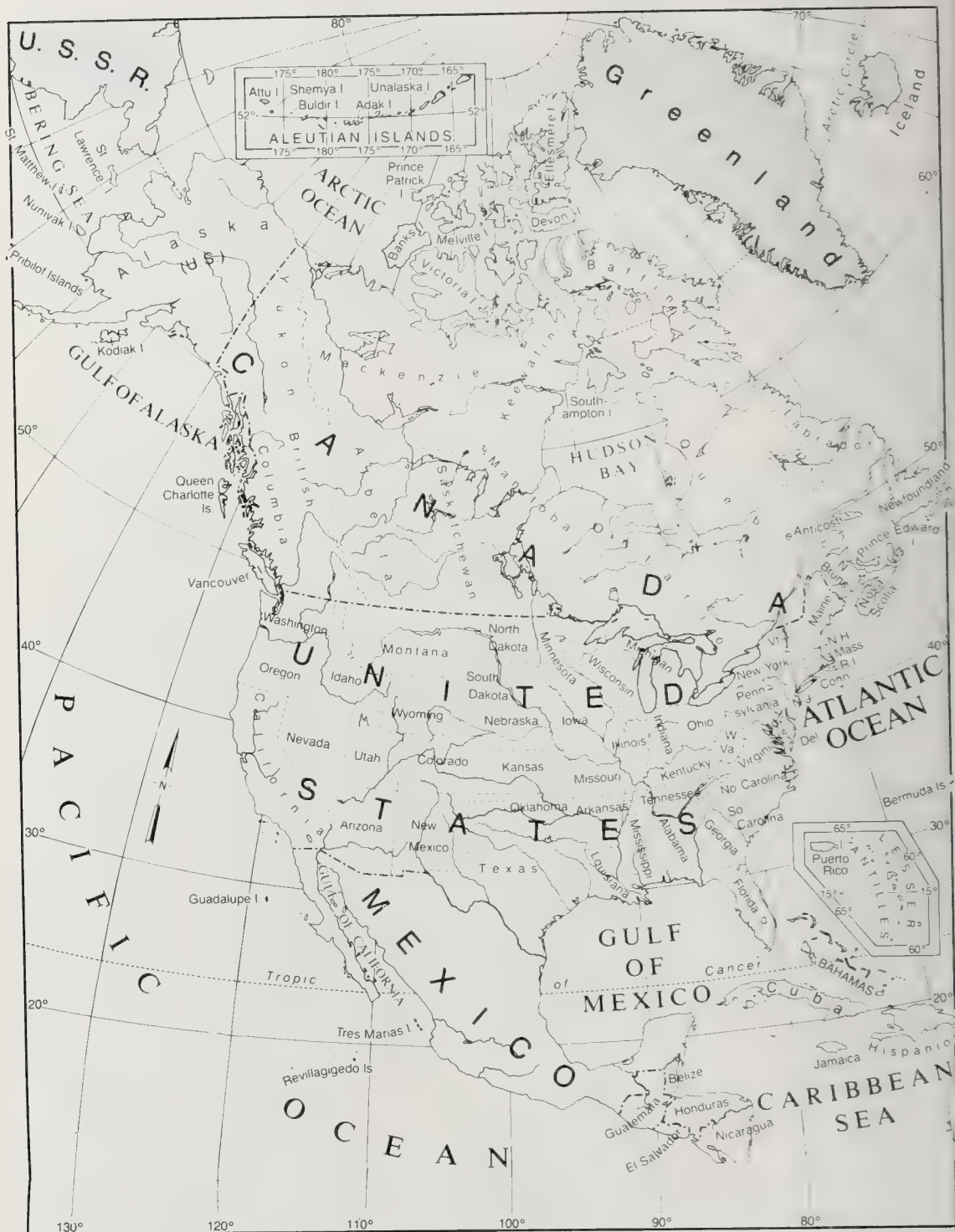
Little of the Northern Plains is forested, and shelterbelts have attracted bird species that not otherwise occur there. Mature shelterbelts resemble a late successional stage of the lowland hardwood forest in the north-central states. Perches for singing and hawking birds are available above the surrounding cropland or grassland. Foliage gleaners utilize the leaves of trees and shrubs. Raptors and hole-nesters are common in old shelterbelts. None of these microhabitats exist without woody vegetation. Now, with the advent of center-pivot irrigation and large grain drills and harvesters, many shelterbelts are being removed.

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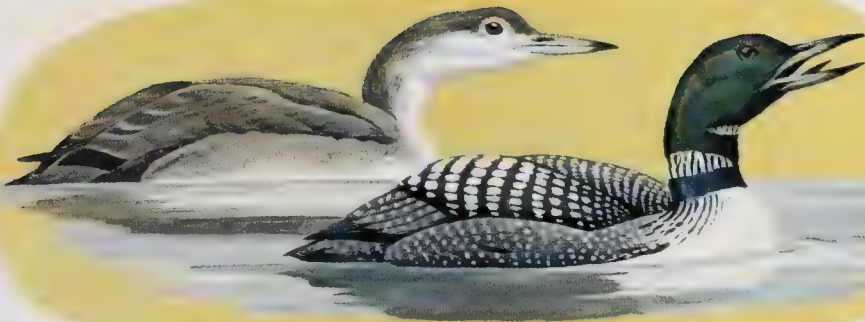
Ranges described in text generally follow boundaries and names shown on this map, modified from the A.O.U. Checklist of North American Birds, 6th Edition, 1983.

Common Loon

Gavia immer

winter

summer



L24 "

RANGE: Breeds from western and central Alaska and the northern Yukon east across Canada to southern Baffin Island and Newfoundland south to northern California (at least formerly), northwestern Montana, North Dakota, and northern Iowa east to southern New England and Nova Scotia. Winters principally along coast from Aleutian Islands south to California, from Newfoundland south to Gulf Coast, and on lakes and bays near coasts. During migration occurs on inland waters throughout most of the United States.

STATUS: Locally common.

HABITAT: Breeds on or near freshwater lakes, ponds, and occasionally riverbanks, from tundra south in either open or wooded habitat. Territories may range from entire lakes of more than 100 acres to bays of 15 to 20 acres.

SPECIAL HABITAT REQUIREMENTS: Bodies of water deep enough to escape from enemies by diving and large enough that it can take flight (up to 1/4 mile).

NEST: Nests on the ground as close to water as possible, on islands, in sheltered places in coves, or on promontories or headlands. May locate nests on bare soil, on floating or matted vegetation, on muskrat houses or on rocks. Same nest site may be used, presumably by same pair, year after year.

FOOD: Captures food during dives underwater. Generally eats approximately 80 percent fish with some crustaceans, vegetable matter, and insects, varying with locale.

REFERENCES: Palmer 1962, Smith 1981, Terres 1980, Vermeer 1973, Wahl in Farrand 1983a.

Pied-billed Grebe

Podilymbus podiceps



RANGE: Breeds in southeastern Alaska and from central Canada south locally through temperate North America. Winters through most of breeding range from southern British Columbia and the central United States southward, casually farther north. Also winters throughout West Indies, Central and South America.

STATUS: Common; most widespread grebe in North America.

HABITAT: Inhabits ponds with much shoreline and emergent vegetation, marshes with areas of open water 15 to 25 inches deep, and marshy inlets and bays. Found on ponds, sloughs, flooded areas, marshy parts of lakes and rivers, and occasionally estuarine waters with weak tidal influence.

SPECIAL HABITAT REQUIREMENTS: Marshes, sluggish streams, ponds 18 acres or less, and some emergent vegetation.

NEST: A solitary nester, with generally only one pair nesting per pothole. Constructs a floating nest usually in shallow water, but sometimes on water several feet deep and well concealed in emergent vegetation. Builds nest around or anchored to reeds, rushes, or bushes and usually within 50 feet of open water.

FOOD: Captures food while swimming and during dives. Primarily eats fishes, but also insects and some crayfish.

REFERENCES: Faaborg 1976, Glover 1953, Palmer 1962, Sealy 1978, Terres 1980, Wetmore 1924.

Horned Grebe

Podiceps auritus

winter summer



L9"

RANGE: Breeds in North America from central Alaska and northern Yukon to northern Manitoba south to eastern Washington, central Wisconsin, and extreme western Ontario. Winters from the Aleutian Islands and southern Alaska along the Pacific Coast to southern California and along the Atlantic Coast from Nova Scotia to southern Florida. During winter primarily marine, off ocean beaches and rocky shores as well as in sheltered inlets and bays. May be found in any water as a migrant.

STATUS: Common in North America except in the Southwest.

HABITAT: Inhabits ponds, marshes, sloughs, backwaters of streams and rivers, shallow bays of large lakes, and flooded places with some open water. Can alight on and take wing from small streams. Early in breeding season, often found where relatively little plant cover extends above water.

SPECIAL HABITAT REQUIREMENTS: Small, shallow potholes of 18 acres or less.

NEST: A solitary nester, with one pair occupying an entire pond. Builds nests commonly in quiet shallow water, usually well within a fringe of emergent vegetation, although sometimes very exposed. The floating, partly submerged nest is anchored to reeds or bushes or to bottom. Prefers to nest in small ponds with open water where territory can be observed visually.

FOOD: Usually feeds in water 5 to 25 feet deep. Food caught during long dives under water consists primarily of small fish, crayfish, amphipods, prawns, shrimp, aquatic and land insects, and some amphibians and leeches; may also include some vegetable matter. In winter, nearly half of diet may be crustaceans.

REFERENCES: Faaborg 1976, Ferguson 1981, Palmer 1962, Robbins et al. 1983, Terres 1980, Wetmore 1924.

Red-necked Grebe

Podiceps grisegena



RANGE: Breeds from western and central Alaska to south-central Ontario south to St. Lawrence Island, the Alaska Peninsula, central Washington to south-central Minnesota; rarely to southwestern Oregon, northern Michigan, southern Quebec and New Hampshire. Winters along Pacific and Atlantic Coasts and casually along Gulf Coast.

STATUS: Populations decreasing or stable.

HABITAT: Inhabits quiet inland waters on prairies, in woodlands, and extending out onto tundra. Less commonly found on prairie sloughs and marshes, backwaters of rivers, and flooded areas.

SPECIAL HABITAT REQUIREMENTS: Shallow lakes and ponds (rarely less than 10 acres per pair) with at least some emergent vegetation.

NEST: Usually a solitary nester although sometimes nests in loose colonies. Constructs an anchored floating nest on water 2 to 3 feet deep within or near edge of emergent vegetation such as cattails, sedges, rushes, and sometimes bushes. Sometimes builds nest on a muskrat house.

FOOD: Dives and feeds in water at or near the bottom. In marshes and lakes, consumes primarily aquatic insects and some fishes. Also takes land insects, crustaceans, mollusks, aquatic worms, amphibians, and some vegetative matter.

REFERENCES: Chamberlin 1977, Palmer 1962, Tate and Tate 1982, Terres 1980.

Eared Grebe

Podiceps nigricollis



RANGE: Breeds from south-central British Columbia and Manitoba south to Baja California and south-central Texas. Winters inland from California, Nevada, Utah, New Mexico, and central Texas and on the Pacific Coast from southern British Columbia south to Guatemala. Casual in eastern United States and also in Old World.

STATUS: Large breeding colonies and winter flocks common.

HABITAT: Inhabits marshy lakes and ponds, and large pools in streams or rivers in the prairie region of North America. Less typically inhabits marshes with some open water. During winter, found on salt lakes, bays, estuaries, and seacoasts.

SPECIAL HABITAT REQUIREMENTS: Freshwater lakes and ponds larger than 18 acres, with shallow margins and emergent vegetation.

NEST: Nests in compact colonies or sometimes singly, in sheltered areas, or in shallow water away from emergent vegetation. Builds a floating nest that is a platform of marsh vegetation built up from the bottom or anchored to reeds.

FOOD: Gleans land insects from surface of water, or captures aquatic insects during dives. Also takes small crustaceans, small fishes, leech eggs, mollusks, and amphibians

REFERENCES: Faaborg 1976, Grinnell and Miller 1944, Low and Mansell 1983, Palmer 1962, Ratti in Farrand 1983a, Terres 1980, Verner and Boss 1980, Wetmore 1924.

Western Grebe

Aechmophorus occidentalis
(includes Clark's Grebe)

Aechmophorus clarkii



L18"

RANGE: Breeds from southeastern Alaska and south-central British Columbia to southwestern Manitoba south to southern California, New Mexico, northwestern Iowa, and western Minnesota. Winters along the Pacific Coast from southern British Columbia to Baja California, and from Utah, Colorado, New Mexico, and western and southern Texas south into Mexico.

STATUS: Locally abundant.

HABITAT: Inhabits fairly extensive areas of open water bordered by tall emergent plants. Found on marshes, lakes, and bays; in winter may be found on salt, brackish, and freshwater where small fishes are abundant.

SPECIAL HABITAT REQUIREMENTS: Open, fresh lakes bordered by rushes or tules.

NEST: Nests in colonies of hundreds, even thousands of pairs at some lakes, but occasionally nests singly. Builds nests in colonies closely spaced, with territories consisting of only immediate vicinity of nest. Constructs nests in extensive areas of open water bordered by tules or rushes, in emergent vegetation, or on dry land. Prefers to nest near or on open shallow water about 12 inches deep. Anchors nests to, or builds on, submerged roots of bulrushes or other plants.

FOOD: Captures food during dives underwater. Consumes primarily fishes. Also takes mollusks, crabs, marine worms, salamanders, and insects.

REFERENCES: Grinnell and Miller 1944, Lindvall and Low 1982, Palmer 1962, Terres 1980, Wetmore 1924.

American White Pelican

Pelecanus erythrorhynchos
(formerly White Pelican)



RANGE: Breeds from south-central British Columbia to central Manitoba and southwestern Ontario south locally to extreme northern California east to northern Colorado, northeastern South Dakota, and southwestern Minnesota. Sporadic on central coast of Texas and from central to southern California. Winters along the Pacific Coast from central California and southern Arizona south to Central America, and from Florida and the Gulf States south; casually throughout breeding range in western North America.

STATUS: Locally common throughout breeding range.

HABITAT: Found primarily on lakes, also rivers, estuaries, and shallow coastal bays and inlets. Loafs on beaches, sandbars, and driftwood.

SPECIAL HABITAT REQUIREMENTS: In freshwater habitat, islands isolated from mammalian predators.

NEST: Nests on the ground in colonies of a few to several hundred pairs on small, relatively flat islands, without tall (over 3 feet) obstructions, with loose earth suitable for heaping into nest mounds. Rarely, nests on floating islands of marsh plants. Colonies prefer open areas of annual grasses and forbs, shrubs, and nonvegetated areas.

FOOD: Primarily consumes fish caught by scooping pouch into water while swimming. Groups often cooperate in fishing. Adults require about four pounds of food daily, and feeding areas may be located far from nesting areas. Also feeds on some salamanders and crayfish.

REFERENCES: Knopf 1979, Knopf and Kennedy 1981, Lingle and Sloan 1980, Palmer 1962, Terres 1980.

Double-crested Cormorant

Phalacrocorax auritus



L 27" W 50"

RANGE: Breeds in the southeastern Bering Sea, southern Alaska, and from southwestern British Columbia and northern Alberta to Newfoundland south along Atlantic and Pacific Coasts; very locally throughout interior of North America. Winters along the Pacific Coast from the Aleutian Islands and southern Alaska south to Baja California and Guerrero; on the Atlantic Coast from New England south; in the Mississippi and Rio Grande Valleys; and along the Gulf Coast south to Central America.

STATUS: Widespread and locally common.

HABITAT: Inhabits coastal areas, bays, estuaries, marine islands, freshwater lakes, ponds, rivers, sloughs, and swamps. (Only cormorant likely to be seen inland around freshwater lakes and rivers.) Has a pronounced preference for perching in trees, on rocks, buoys, or other objects that overhang or project from the water.

SPECIAL HABITAT REQUIREMENTS: Undisturbed nesting site and convenient, dependable food source within a foraging radius of 5 to 10 miles from roost or colony.

NEST: Nests in colonies of a few to 3,500 pairs on rocky islands, cliffs facing water, or in stands of live or dead trees in or near water. In the Northeast and along the Pacific Coast, nests on the ground, on rocky islands, or on cliffs. Inland and in Florida, usually nests in trees. Breeding colonies may be located from below sea level to over 5,600 feet.

FOOD: Captures food during dives in water, generally 5 to 25 feet deep but sometimes up to 72 feet deep. Prefers to hunt in water with a sandy bottom rather than over a rocky or gravelly bottom. Consumes primarily saltwater fish of little commercial value, plus freshwater yellow perch, bullheads, sticklebacks, carp, crappies, and sunfish. Also eats some salamanders, crustaceans, reptiles, mollusks, and sea worms.

REFERENCES: Palmer 1962, Stallcup in Farrand 1983a, Terres 1980.

Anhinga

Anhinga anhinga



RANGE: Breeds from central and eastern Texas east to coastal North Carolina and south to southern Brazil and Ecuador. Winters in southeastern United States from central South Carolina, Georgia, Florida, and the Gulf Coast southward. Occasionally disperses north of breeding range.

STATUS: Common throughout range.

HABITAT: Inhabits quiet or slow-moving, often rather murky waters. Usually found in wooded freshwater swamps, streams, or tree-fringed lakes with water lilies, lotus, and other aquatic vegetation. Found in cypress swamps, freshwater sloughs of sawgrass and reeds with scattered willow clumps, or mangrove-bordered salt and brackish bays, lagoons, and tidal streams. Primarily a freshwater bird, but will range to marine coasts. Often perches with wings partly extended to dry.

SPECIAL HABITAT REQUIREMENTS: Quiet, sheltered waters with some trees for perching.

NEST: Nests in small groups with herons and egrets. May appropriate nests of common and snowy egrets or little blue herons, or construct its own. Nests are usually 3 to 10 feet above water.

FOOD: Catches food by diving under water from the surface, while flying over water, or from a perch. Eats primarily fish, but also takes aquatic insects, crayfish, shrimp, leeches, tadpoles, frog eggs, water snakes, young alligators, and small terrapins.

REFERENCES: Oberholser 1974a, Palmer 1962, Pough 1951, Sykes in Farrand 1983a, Terres 1980.

American Bittern

Botaurus lentiginosus



L 23" W 45"

RANGE: Breeds from extreme southeastern Alaska, central British Columbia, and southern Mackenzie to central Quebec and Newfoundland south to southern California, New Mexico, Texas, and Florida. breeds rarely south of northern California, Utah, Plains States, Ohio River Valley, and Virginia. Winters from southern British Columbia, Utah, New Mexico, central parts of Gulf States, and southern New England south to southern California, Gulf of Mexico, and along Atlantic Coast.

STATUS: Rather common, but elusive.

HABITAT: Inhabits freshwater or saltwater marshes, bogs, swamps, wet meadows, or wherever the ground is wet and tall, emergent vegetation such as cattails, bulrushes, and reeds are present. Usually perches on the ground, sometimes on a log or stump, or on cattails 3 to 4 feet above water, rarely in trees. Generally solitary; will freeze with neck and bill pointing upward, blending into marsh vegetation.

SPECIAL HABITAT REQUIREMENTS: Wetlands with tall, emergent vegetation.

NEST: Usually a solitary nester, but may form loose colonies in favorable habitat. Typically nests on flimsy platform of cattails, reeds, or sedges, 4 to 5 inches above water in emergent vegetation, occasionally on the ground among grasses or in shrubs.

FOOD: Stalks food in marshes, meadows, along edges of shallow ponds, or wherever the ground is wet. Also searches for grasshoppers in dry meadows. Consumes mollusks, spiders, crustaceans, fish, frogs, salamanders, snakes, lizards, small birds, small mammals, eels, and land and aquatic insects.

REFERENCES: Armistead in Farrand 1983a, Grinnell and Miller 1944, Low and Mansell 1983, Palmer 1962, Robbins et al. 1983, Weller 1961.

Least Bittern

Ixobrychus exilis

L 11" W 17"



RANGE: Breeds locally from southern Oregon to central Baja California and southern coastal Sonora in the west; in the east across Canada from southern Manitoba, southern Ontario, and southern New Brunswick south to Texas, the Gulf Coast, Florida, and the Greater Antilles. Winters from southern California, southern Texas, and northern Florida south to Panama and Colombia.

STATUS: Locally common, but elusive.

HABITAT: Inhabits freshwater marshes, bogs, and swamps with dense cattails, reeds, bulrushes, buttonbush, sawgrass, smartweeds, arrowheads, and other tall aquatic and semi-aquatic vegetation. Prefers marshes with scattered bushes or other woody growth. Less commonly found in coastal brackish marshes and mangrove swamps. Usually is hidden in tall vegetation, and slips away by walking or climbing through reeds or even by running through them 2 to 3 feet above water, grasping a single reed or several in each foot.

SPECIAL HABITAT REQUIREMENTS: Freshwater wetlands surrounded by tall aquatic vegetation.

NEST: Nests singly in dense stands of emergent vegetation 6 to 24 inches above water that is 3 to 38 inches deep, and close to open water. Uses natural clump of the previous year's vegetation to form the foundation of the nest. Occasionally nests in bushes, and more rarely, on the ground.

FOOD: Feeds on the open water side of emergents, and captures small fish. Also takes frogs, tadpoles, salamanders, leeches, mollusks, crustaceans, insects, lizards, slugs, and occasionally small mammals.

REFERENCES: Low and Mansell 1983, Palmer 1962, Terres 1980, Weller 1961.

Great Blue Heron

Ardea herodias

L38"



RANGE: Breeds from southern Alaska, coastal and southern British Columbia, southern Keewatin, and central Manitoba east to Nova Scotia and south, except in high mountains. Winters from southern-coastal Alaska, coastal British Columbia, central United States, and southern New England south to northern South America.

STATUS: Common throughout range.

HABITAT: Inhabits a wide variety of freshwater and saltwater habitats including ponds, lakes, streams, rivers, marshes, wet meadows, tidal flats, sandbars, and shallow bays, or wherever shallow water or marsh vegetation is present.

SPECIAL HABITAT REQUIREMENTS: Open water or wetland habitats.

NEST: Generally nests in colonies, preferably in an isolated patch of woodland or on an island. Builds nests in the tops of the tallest trees, live or dead, often above 50 feet, but also in bushes, on rock ledges, sea cliffs, in tule rushes, and on the ground. In colonies, may build dozens of nests, which are used repeatedly, in the crown of the same tree. In mixed heronries, typically nests in highest parts of trees while other heron species occupy lower parts of same trees. May travel as far as 10 miles from nest sites to foraging areas.

FOOD: Usually stands motionless in shallow water and waits until prey comes within striking distance. Also forages in wet meadows, pastures, dry fields, and even along road shoulders and in suburban ponds. Consumes small fishes, frogs, salamanders, lizards, snakes, shrimp, crabs, crayfish, aquatic and land insects, leeches, and small mammals.

REFERENCES: Low and Mansell 1983, Palmer 1962, Pough 1951, Sykes in Farrand 1983a, Terres 1980, Verner and Boss 1980.

Great Egret

Casmerodius albus
(formerly Common Egret)



L32"

RANGE: Breeds from southern Oregon and southern Idaho south to southwestern Arizona, and from southeastern Saskatchewan, southwestern Manitoba, southern Ontario, and Maine south through the Gulf States to South America. Disperses after breeding to the north into Washington, Michigan, southern Ontario and Quebec, and the Maritime Provinces. Winters from northern California across southern United States, and south along Atlantic Coast from New Jersey through South America.

STATUS: Common throughout range.

HABITAT: Inhabits streams, ponds, lakes, rice fields, freshwater and saltwater marshes and lagoons, and mud flats. After feeding during day, flies singly or in small groups to a communal roost in trees or shrubbery. Gregarious during all seasons.

SPECIAL HABITAT REQUIREMENTS: Open water or wetland habitats near woodlands.

NEST: Nests singly or in colonies, often with other herons, ibises, wood storks, cormorants, and anhingas. Usually nests in woods or thickets near water so long as there is adequate support for the nest. Builds nest from 1 to 40 feet above ground, depending on substrate. Sensitive to disturbance by people when nesting and may flush at the slightest provocation.

FOOD: Forages in freshwater, brackish, or saltwater swamps, along streams, and in ponds. Consumes fishes, frogs, salamanders, snakes, snails, crustaceans, insects, and small mammals.

REFERENCES: Grinnell and Miller 1944, Low and Mansell 1983, Palmer 1962, Sykes in Farrand 1983a, Terres 1980.

Snowy Egret

Egretta thula

L20"



RANGE: Breeds from northern California and Montana south to central and eastern Texas, along the lower Mississippi Valley, and from Maine south along the Atlantic and Gulf Coasts to South America. After breeding, disperses north to Oregon, Nebraska, Great Lakes, and Atlantic Canada. Winters from northern California, southwestern Arizona, the Gulf Coast, and coastal South Carolina south throughout the breeding range.

STATUS: Common; breeding range expanding northward.

HABITAT: Inhabits ponds; borders of lakes; freshwater, brackish, and saltwater marshes and swamps; stream courses; tidal flats; rice fields; and sometimes dry fields, where it associates with cattle.

NEST: Nests in colonies (many coastal), sometimes with thousands of pairs or in smaller colonies with other herons, ibises, cormorants, and anhingas, or even singly. In western United States, commonly nests on the ground in cattail marshes; in other areas, may nest up to 30 feet high in trees and shrubs.

FOOD: Forages by rushing about and shuffling its feet in shallow water to flush its prey out of hiding. Consumes small fish, frogs, lizards, snakes, shrimp, fiddler crabs, crayfish, grasshoppers, cutworms, and aquatic insects.

REFERENCES: Grinnell and Miller 1944, Low and Mansell 1983, Palmer 1962, Sykes in Farrand 1983a, Terres 1980.

Little Blue Heron

Egretta caerulea

im.



RANGE: Breeds from southeastern New Mexico to central Kansas, southern Arkansas, southeastern Missouri, southwestern Kentucky, northwestern Tennessee, central Alabama, southern Georgia, and along the Atlantic Coast from Maine, south to the West Indies and South America; sporadically in central Minnesota. After breeding, disperses north in interior to North and South Dakota, Michigan, southern Ontario and southern Quebec, and to Nova Scotia on Atlantic Coast. Winters from southern Baja California, the Gulf Coast, and coastal Virginia south throughout most of breeding range.

STATUS: Common; range is expanding.

HABITAT: Prefers freshwater ponds, lakes, marshes, meadows, and marshy shores of streams, but also inhabits brackish and saltwater coastal habitats. Roosts in trees and shrubs at night.

SPECIAL HABITAT REQUIREMENTS: Open water or wetland habitats.

NEST: Nests in colonies of up to 100 in a variety of trees, usually hardwoods, almost invariably over or by freshwater. Tends to nest on the fringe of mixed colonies, often in company with the tricolored heron. Builds a flimsy platform nest, sometimes as high as 40 feet in trees and shrubs. Nests in willows, buttonbush, red maples, myrtles, and swamp privet.

FOOD: Forages in a slow, methodical manner ashore, in mud, or in very shallow water; not given to wading as deeply as some herons. Seldom feeds in saltwater. When water disappears from marshes and swamps, will live solely on insects caught in grasslands. Diet includes fishes, frogs, lizards, snakes, turtles, shrimp, fiddler crabs, crayfish, aquatic insects, spiders, grasshoppers, crickets, and beetles.

REFERENCES: Low and Mansell 1983, Palmer 1962, Sykes in Farrand 1983a, Terres 1980.

Cattle Egret

Bubulcus ibis

im.



L17"

RANGE: Breeds locally from northwestern and central California, southern Idaho, northern Utah, Colorado, North Dakota, southern Saskatchewan, Minnesota, Wisconsin, southern Ontario, northern Ohio, and Maine south to Florida, West Indies, and Central and South America. After breeding, disperses north to southern British Columbia, southcentral Canada, and the Maritime Provinces. Winters throughout most of breeding range.

STATUS: Common; a recent immigrant from the Old World, range is rapidly expanding.

HABITAT: Frequents a great variety of habitats including pastureland, freshwater and salt marshes, fallow and plowed fields, orchards, citrus groves, road shoulders and median strips, vacant lots, lawns, and other open grassy areas. Least shy and least aquatic of North American herons; usually found in close association with large hoofed mammals, particularly cattle, and often perching on their backs.

SPECIAL HABITAT REQUIREMENTS: Wetlands for nesting.

NEST: Nests colonially, often with other herons and ibises, in both freshwater and saltwater habitats, on islands, in willows and tamarisks along watercourses, occasionally in cypress swamps with a lower growth of buttonbush, or in scrub oaks in marshlands. Also nests in redcedar, red maple, and in pines. Usually builds nests at heights of 5 to 12 feet, up to 30 feet in heronries.

FOOD: Usually feeds in dry or moist open pastures among livestock, capturing insects and other prey disturbed as cattle walk and graze. May glean ticks or bugs off cattle. Consumes grasshoppers, leopard and cricket frogs, spiders, and some toads.

REFERENCES: Palmer 1962, Sykes in Farrand 1983a, Terres 1980.

Green-backed Heron

Butorides striatus

(formerly Green Heron)



RANGE: Breeds from southwestern British Columbia to northern California, southern Nevada and Utah, and north-central New Mexico, and from the western edge of the Great Plains States, southern Ontario and southern New Brunswick south to eastern Panama. After breeding, disperses north to eastern Washington, Idaho, and southern Canada. Winters from western Washington, coastal and southeastern California, southern Arizona, Texas and Louisiana, and northern Florida and South Carolina south to South America.

STATUS: Common, locally abundant.

HABITAT: Found in a wide variety of freshwater and saltwater habitats, primarily those in riparian deciduous zones. These include wet woodlands, lakeshores, ponds, rivers, streams, swamps, and marshes. Commonly alights on trees, stumps, or submerged debris, but roosts on or close to the ground.

SPECIAL HABITAT REQUIREMENTS: Wetlands or open water habitats.

NEST: Generally a solitary nester, but sometimes nests in colonies of 6 pairs or more. Nest may be built away from water in dry woodlands and orchards, on a low tussock or muskrat house, or in trees near water, often a dense tangle in crowns of middle-aged trees, typically 10 to 15 feet above ground, but up to 30 feet.

FOOD: Captures prey while standing and waiting in shallow water, or by walking slowly, typically in a crouched position. Consumes fish, frogs, crayfish, mollusks, prawns, insects, leeches, earthworms, small snakes, snails, and mice.

REFERENCES: Low and Mansell 1983, Palmer 1962, Terres 1980, Verner and Boss 1980.

Black-crowned Night-Heron

Nycticorax nycticorax



RANGE: Breeds from central Washington and east-central Alberta to southern Quebec, northeastern New Brunswick and Nova Scotia south locally through the United States to South America. Wanders a great deal. After breeding, disperses over most of the United States not within its breeding range, except northern Rocky Mountain region, and north into Canada. Winters in the Southwest and the lower Ohio Valley, Gulf Coast, and southern New England south throughout the breeding range.

STATUS: Common throughout most of its range.

HABITAT: Inhabits a wide variety of freshwater, brackish, and saltwater habitats almost anywhere a wader might exist, including lakes, ponds, marshes, wooded swamps, slow streams with pools, or rivers. Roosts by day, usually in a well-foliaged tree, not necessarily near feeding grounds.

SPECIAL HABITAT REQUIREMENTS: Open water or wetland habitats.

NEST: Nests in small to large colonies, usually with other heron species, in almost any habitat: wooded areas near coastal marshes, spruce groves on marine islands, hardwood forests on offshore islands, swamps, cattail marshes on prairies, clumps of tall grass on dry ground, apple orchards, and sometimes in city parks. Nests close together on the ground to over 160 feet high in trees, and may be well concealed or in the open.

FOOD: Forages mainly at night, by standing and waiting, or walking slowly along shallow margins of lakes, mud-bordered bays, and in marshy places where there is standing or slow-running water. Eats fish, frogs, tadpoles, salamanders, snakes, toads, crayfish, crabs, shrimp, squid, clams, mussels, dragonflies, algae, succulent plants, young birds, and small mammals.

REFERENCES: Grinnel and Miller 1944, Low and Mansell 1983, Palmer 1962, Sykes in Farrand 1983a, Terres 1980, Verner and Boss 1980.

Yellow-crowned Night-Heron

Nycticorax violaceus



L 21" W 44"

RANGE: Breeds from central and northeastern Texas to southern Nebraska, southeastern Minnesota, east to the lower Ohio Valley, and eastern Tennessee, southeastern Pennsylvania and Massachusetts south to South America. After breeding, disperses north to eastern Colorado, Iowa, southern Ontario, and Atlantic Canada. Winters from the Gulf Coast and coastal South Carolina south throughout breeding range.

STATUS: Much less common than black-crowned night-heron.

HABITAT: Inhabits both freshwater and saltwater habitats, usually lush river swamps, but also tidal flats, stagnant backwaters or bayous of large cypress swamps, mangrove swamps, or dry, rocky, almost waterless areas on certain islands.

SPECIAL HABITAT REQUIREMENTS: Wooded swamps.

NEST: Nests in small to large colonies, sometimes with black-crowned, little blue, tricolored, and great blue herons, or singly, in trees or bushes and sometimes on the ground. Often nests in willows close to water, in mangroves, or in baldcypresses, usually 15 to 20 feet above ground.

FOOD: Hunts at night but also frequently by day. Unlike other herons, rarely takes fishes, but feeds largely on crustaceans, mainly crayfish, and land and fiddler crabs. Also eats mussels, frogs, aquatic insects, snails, small snakes, lizards, leeches, and terrapins.

REFERENCES: Low and Mansell 1983, Palmer 1962, Sykes in Farrand 1983a, Terres 1980.

Glossy Ibis

Plegadis falcinellus



L19"

RANGE: Breeds locally from Maine and Rhode Island south to Florida, and west on the Gulf Coast to Louisiana. Also inland, at least casually, in Arkansas. Wanders, at least, casually, to the Midwest and southern Canada. Winters from northern Florida and the Gulf Coast of Louisiana south to South America.

STATUS: Locally common; initially an irregular breeding bird in North America in small colonies along Atlantic Coast, but recently has increased in numbers.

HABITAT: Found in freshwater, brackish, and saltwater habitats, primarily marshes and estuaries. Prefers shallow pools bordered by shrubs and emergent vegetation.

SPECIAL HABITAT REQUIREMENTS: Wetlands.

NEST: Nests in small colonies, usually with herons or other waders in a variety of habitats; in willows or mixed growths of mangroves, tropical buttonwood and salt myrtle in Florida; in willows, gum, swamp maple, bay and buttonbush in cypress swamps of South Carolina; on islands of tamarisk, waxmyrtle, and salt myrtle; in cordgrass; in mixed stands of holly, redcedar, bayberry, wild cherry, sumac, salt myrtle, Virginia creeper, wild grape, and cat greenbrier on barrier beaches along New Jersey Coast; and in cattail marshes. Nests on platforms on the ground in marshes, up to 10 feet high in shrubs and trees growing in water, in sites well covered with vegetation.

FOOD: Forages by probing in soft mud flats and in flooded fields. Eats mostly crayfish, but also snakes, grasshoppers, cutworms and other grubs, and leeches.

REFERENCES: Burger and Miller 1977, DeGraff et al. 1980, Low and Mansell 1983, Palmer 1962, Terres 1980.

White-faced Ibis

Plegadis chihi

L19"



RANGE: Breeds locally from central California, eastern Oregon, southern Idaho, Montana, southern North Dakota, and southwestern Minnesota south to Mexico; and from eastern Texas, southern Louisiana east occasionally to Florida. Wanders, at least casually, north to southern Canada. Winters from southern California and the Gulf Coast of Texas and Louisiana south to Mexico.

STATUS: Uncommon; nesting populations have been greatly reduced due to use of pesticides and herbicides by rice farmers.

HABITAT: Inhabits wetland habitats, preferably marshes and sloughs or ponds surrounded by low bushes or willows, and emergent vegetation such as bulrushes. Also in tule or bulrush swamps, in centers of ponds, and in irrigated rice fields. Roosts in marshes in the evenings.

SPECIAL HABITAT REQUIREMENTS: Freshwater marshes and sloughs.

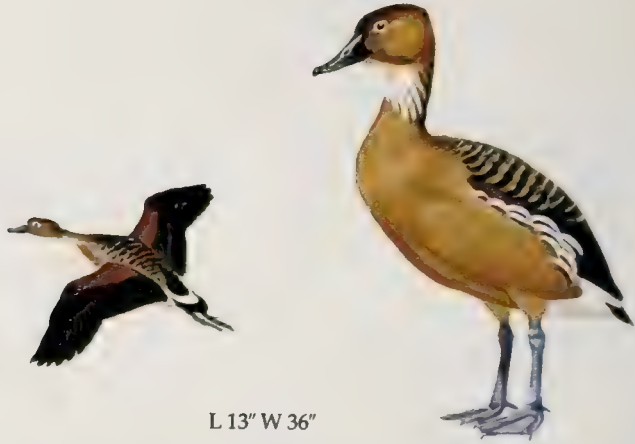
NEST: Colonial nester, sometimes with or near colonies of great blue and black-crowned night-herons, or snowy egrets. Generally nests in large beds of bulrushes or reeds several feet above water; on floating mats of dead plants, in cattails and hardstem and alkali bulrush; or infrequently on dry land. On land, prefers to nest on the ground among low shrubs and mixed forbs rather than in grass or cactus. Generally nests in areas well covered with vegetation.

FOOD: Feeds by probing in freshwater marshes. Consumes insects, newts, leeches, worms, mollusks, crustaceans (especially crayfish), frogs, fishes, and some snails. After nesting season, feeds in larger marshes as well as in irrigated fields.

REFERENCES: Burger and Miller 1977, Oberholser 1974a, Palmer 1962, Ryder 1967, Terres 1980.

Fulvous Whistling-Duck

Dendrocygna bicolor



L 13" W 36"

RANGE: Breeds from southern California to southwestern Arizona, and from central and eastern Texas and the Gulf Coast of Louisiana, south to Mexico; locally in southern Florida. Wanders sporadically throughout North America. Winters from southern California, southern Arizona, the Gulf Coast, and southern Florida south to Mexico.

STATUS: Fairly common, but population levels fluctuate.

HABITAT: Inhabits marshlands, wet meadows, and in North America, primarily flooded agricultural land and rice fields. Does not ordinarily frequent woodlands. Loafs among dense bulrushes or far out on marshy ponds.

SPECIAL HABITAT REQUIREMENTS: Broad, open marshlands.

NEST: Prefers to nest in rice fields on low, contour levees, as well as a few inches over water among rice plants and wood growing between levees. Also nests in bulrushes, in knotgrass and dense beds of cattails, on hummocks in marshes, at the edge of ponds and swamps, or in rank tall grasses of wet meadows; rarely in tree cavities.

FOOD: Feeds primarily at night, walking about on land gleaning seeds of grasses and weeds. Also tips up in shallow water, and visits cornfields for waste grain. Has a mainly vegetarian diet that includes rice, millets, nutgrass, knotgrass, signalgrass, water shield, and alfalfa.

REFERENCES: Baldwin et al. 1964, Bellrose 1976, Cottam and Glazner 1959, Terres 1980, USDA 1981.

Black-bellied Whistling-Duck

Dendrocygna autumnalis



L 13" W 37"

RANGE: Resident in southern Arizona, central and southeastern Texas, and south into South America.

STATUS: Rather common within its breeding range, but only a straggler outside.

HABITAT: Prefers open woodlands, groves or thicket borders of ebony, mesquite, retama, huisache, and cacti near banks and shallows of rivers, ponds, or marshes. In semiarid southern Texas, it has adapted to some constructed "water habitats" such as small reservoirs and stock tanks. May loaf on shores of small ponds and frequently perches in trees; usually does not alight or swim on deep water.

SPECIAL HABITAT REQUIREMENTS: Shallow waters or wetlands, and natural cavities in trees or depressions in ground near water for nesting.

NEST: Nests in cavities of elms, willows, live oaks, ebony, mesquite, hackberry, and other trees; also in nest boxes and on the ground. Nest trees may be standing in or located up to 3,000 feet from water, while ground nests are usually in grazed brush pastures, well hidden under low shrubs, and usually near water. Uses natural cavities with entrance holes ranging from 4 by 4.75 inches to 7 by 12.5 inches, and located about 9 feet above ground or water.

FOOD: Often feeds at night by grazing in stockyards, pastures, or fields, or by tipping or standing in shallow water. Has a primarily vegetarian diet that includes many cultivated plants, stock foods, and native plants. Consumes about 8 percent animal material, including insects, mollusks, and snails.

REFERENCES: Baldwin et al. 1964; Bellrose 1976; Bolen 1967a, 1967b; Bolen and Forsyth 1967; Johnsgard 1975b; Meanley and Meanley 1958; Terres 1980.

Tundra Swan

Cygnus columbianus

(formerly Whistling Swan and Bewick's Swan)



L36"

RANGE: Breeds from northwestern Alaska south to St. Lawrence Island and the Alaska Peninsula, and east near the Arctic Coast of Baffin Island, thence south around Hudson Bay to Churchill and the Belcher Islands. Winters mainly near coast from southern Alaska through British Columbia to Pacific states and northern Baja California (casual); also in southern Great Basin to northern New Mexico; and in mid-Atlantic states, rarely on Gulf Coast.

STATUS: The most common and widespread swan in North America.

HABITAT: Inhabits lakes, ponds, sluggish streams, and occasionally swamp bogs on open tundra while breeding; may be found along coastal estuaries when not breeding. During winter, primarily found on sizeable reservoirs; shallow, productive lakes of the interior; other sheltered freshwater habitats; or on coastal bays and estuaries.

SPECIAL HABITAT REQUIREMENTS: Open water or wetlands on Arctic tundra.

NEST: Builds nests on the ground along water's edge, on hummocks in marshes or tidal meadows, or on low hills up to one-half mile from water; seems to prefer to nest on small islands in shallow tundra pools. Rarely nests on level stretches in marsh or meadow areas.

FOOD: Feeds by plunging head under water and uprooting aquatic vegetation, preferably in shallow water, and occasionally by tipping up in deeper water, or by grazing in fields. Most commonly eats aquatic plants, but also eats waste corn, soybeans, shoots of winter wheat, grasses, sedges, and thin-shelled mollusks.

REFERENCES: Bellrose 1976, Terres 1980, Tohish in Farrand 1983a, Verner and Boss 1980, USDA 1981.

Trumpeter Swan

Cygnus buccinator



RANGE: Breeds locally throughout Alaska and from southern British Columbia and southwestern Saskatchewan south to southeastern Oregon, eastern Idaho and northwestern Wyoming. Was introduced and is now established at Ruby Lake in Nevada and in southwestern South Dakota. Winters from southern Alaska, western British Columbia, southern Alberta (rarely) and Montana south to northern (casually southern) California, occasionally to Utah, New Mexico, and eastern Colorado.

STATUS: Once near extinction, the population has increased to more than 4,000 birds.

HABITAT: Typically found in open boreal forest; prefers large shallow, fertile marshes or lakes (up to 4 feet deep) with a profusion of submerged and emergent aquatic plants, and generally untimbered but well-vegetated shorelines. During winter, prefers shallow lakes, streams, and ponds with open water that are bordered by some level and open terrain.

SPECIAL HABITAT REQUIREMENTS: Shallow, sheltered waters that do not have a fluctuating water level, and some margins of emergent vegetation.

NEST: Nests on the ground on any site above the general level of the marsh terrain, preferably on muskrat houses surrounded by water 1 to 3 feet deep. Also nests on shore in sedges, bulrushes, cattails, rushes, or in horsetail. Has a nesting territory that ranges from 70 acres along irregular shorelines to 150 acres along straight shorelines.

FOOD: Feeds primarily in shallow waters of lakes or open marsh, digging up roots and tubers of aquatic plants, or snapping off plant parts with bill; rarely feeds on land. Eats a variety of marsh and aquatic plants.

REFERENCES: Banko 1960, Bellrose 1976, Johnsgard 1975b, Terres 1980, Van Wormer 1972.

Greater White-fronted Goose

Anser albifrons



L20"

RANGE: Breeds from northern Alaska south to Bristol Bay and Cook Inlet, and east across northern Yukon, northern Mackenzie and southern Victoria Island to northern Keewatin. Winters from southern British Columbia south along the coastal states; on the Gulf Coast from Texas and Louisiana south to Mexico; and rarely in the lower Mississippi Valley from Missouri southward.

STATUS: Common throughout range.

HABITAT: Inhabits the borders of shallow marshes and lakes, riverbanks and islands, deltas, dry knolls, and hills near rivers and ponds in Arctic tundra. Generally found in areas characterized by dwarf birch, willows, bilberries, crowberries, Labrador tea, cassiope, raspberries, dryas, sedges, horsetails, cottongrasses, bluegrass, fescue, arctic grass, sphagnum moss in depressions, and reindeer moss and cetaria on drier sites. Rests on shallow ponds and sloughs in marshes. Winters in sheltered inland and coastal marshes and on open terrain and pasturelands with small bodies of water.

SPECIAL HABITAT REQUIREMENTS: Wetlands in Arctic tundra.

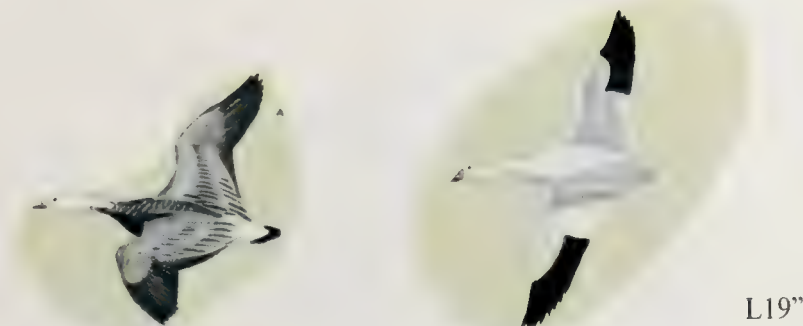
NEST: Typically nests in depressions on the ground in tall grass bordering tidal sloughs or in sedge marshes, usually within 300 feet of water, or on hummocks along rivers, streams, and lakes. Generally does not nest in colonies but may be found in loose colonies of 15 to 20 pairs in favored locations.

FOOD: Primarily grazes on marsh grasses, freshly sprouted grain in fields, and fresh growth in burned-over pastures. Sometimes feeds heavily on aquatic plants and in grain fields after harvest. In the Arctic, consumes tundra plants, aquatic insects and their larvae, and berries.

REFERENCES: Bellrose 1976, Dzubin et al. 1964, Johnsgard 1975b, Pough 1951, Terres 1980.

Snow Goose

Chen caerulescens



RANGE: Breeds from northern Alaska east along the Arctic Coast and islands of Canada to Baffin Island, south to Southampton Island and along both coasts of Hudson Bay to the head of James Bay. Winters from the Puget Sound of British Columbia and Washington south to the interior valleys of California and Mexico; in southern New Mexico; from Kansas and Missouri south to the Gulf Coast; and along the Atlantic Coast from New York to Florida. During migration, found on large staging areas in the Dakotas, Minnesota, Iowa, and Nebraska.

There are two races of the snow goose, the “lesser” and the “greater.” The lesser snow goose has two color phases—a dark phase, or blue goose, and a white phase—while the greater is believed to only have a white phase, and generally breeds farther north than the lesser.

STATUS: Locally abundant.

HABITAT: Inhabits islands of the Canadian Arctic Archipelago or is found within 5 miles of salt water on flat tundra of marsh grasses and sedges, in limestone basins, on islands of river deltas, or on plains usually drained by large rivers that open early in the season. During winter, uses both freshwater and saltwater marshes and wet prairies.

SPECIAL HABITAT REQUIREMENTS: Wetlands on arctic tundra.

NEST: Nests in a shallow depression on the ground in large, loose colonies, on dry sites, primarily in unspoiled, primitive areas. Nests, well concealed by tundra grasses and sedges, as close as 15 to 20 feet from each other on flat land.

FOOD: Feeds by browsing in cultivated fields on winter wheat, in pastures on sprouting grasses, or on waste grain in stubble fields, also by digging out bulbous roots and soft parts of sedges, rushes, marsh grasses, and aquatic plants.

REFERENCES: Bellrose in Farrand 1983a, Cooch 1964, Lemieux 1959, Terres 1980, Verner and Boss 1980.

Ross' Goose

Chen rossii

L16"



RANGE: Breeds primarily in the Queen Maud Gulf area of northern Mackenzie and northwestern Keewatin, but also on southern Southhampton Island and along the west coast of Hudson Bay south to Cape Churchill. Winters almost exclusively in the Central Valley of California and the Salton Sea; also in small numbers along the Rio Grande, New Mexico, and Gulf Coast of Texas.

STATUS: Rare a few decades ago, now quite abundant in recent years.

HABITAT: Inhabits island-studded lakes and deltas of low tundra country. Prefers islands that rise 10 to 20 feet above water level, are covered with rocks and shrubs interspersed with areas of open, level ground, and are surrounded by shallow water (under 5 to 6 feet deep) extensive enough to discourage predators from swimming across. During winter, found on freshwater and brackish marshes and on wet prairies, often in association with the snow goose.

SPECIAL HABITAT REQUIREMENTS: Islands in Arctic tundra lakes.

NEST: Nests on the ground in loose colonies, preferably on islands in mixed habitats of dwarf birch and rocks, or occasionally along river or lake shores if islands are unavailable.

FOOD: Eats grain and new green growth of grasslands and grain fields.

REFERENCES: Barry 1964, Bellrose in Farrand 1983a, Johnsgard 1975b, Ryder 1967, Terres 1980.

Canada Goose

Branta canadensis



L16-26"

RANGE: Breeds from the Arctic Coast of Alaska and northern Canada east to Baffin Island, south to central California, east to western Tennessee, southern Ontario and Quebec, and Newfoundland. Winters from south-coastal and southeastern Alaska, British Columbia and southern Alberta east to the Atlantic Coast of Newfoundland, and south to Mexico, the Gulf Coast and northern Florida.

STATUS: Common; 11 subspecies of the Canada goose are currently recognized.

HABITAT: Found in a variety of habitats near water, from forested and prairie regions to tundra, breeding on swamps, marshes, meadows, rivers, banks of lakes and ponds, and on islands. Winters in tidewater areas, marshes, inland refuges, and in flooded fields.

SPECIAL HABITAT REQUIREMENTS: Elevated habitat feature or artificial structures near water for nesting.

NEST: Usually nests on the ground near water (generally within 150 feet), preferably on a slightly elevated site that is isolated and affords good visibility of the surrounding area. Prefers muskrat houses for nesting but will also nest on small islands lacking tall growth, haystacks, rocky cliffs, hummocks, ridges of silt, pond banks, beaver lodges, and occasionally abandoned nests of ospreys, ravens, owls, or herons. Has successfully adapted to nesting on artificial structures.

FOOD: Essentially a grazer, preferring young, green tender plants. Consumes various grasses and forbs, both terrestrial and aquatic. Consumes agricultural crops as primary food during migration and winter. Also consumes small amounts of insects, insect larvae, mollusks, and small crustaceans.

REFERENCES: Bellrose 1976, Hansen and Nelson 1964, Terres 1980, VanWormer 1968.

Wood Duck

Aix sponsa



RANGE: Breeds in western North America from southern British Columbia and southwestern Alberta south to central California and western Montana; in eastern North America from east-central Saskatchewan east to Prince Edward Island and Nova Scotia south (east of the Rockies) to central and southeastern Texas and the Gulf Coast. In the West, winters irregularly throughout the breeding range; in the East, winters primarily in the southern parts of the breeding range.

STATUS: Common; population has increased in recent years primarily because of the availability of artificial nest structures and protection for most of the year.

HABITAT: Inhabits woodlands near shallow, quiet inland lakes, swamps, river bottoms, ponds, marshes, and streams where nest sites are available. Important forest types are central and southern floodplain forests, red maple swamps, temporarily flooded oak forests, and northern bottomland hardwoods. Prefers areas with many perching sites.

SPECIAL HABITAT REQUIREMENTS: Nest holes in trees or nest boxes in or near still or slow-moving water.

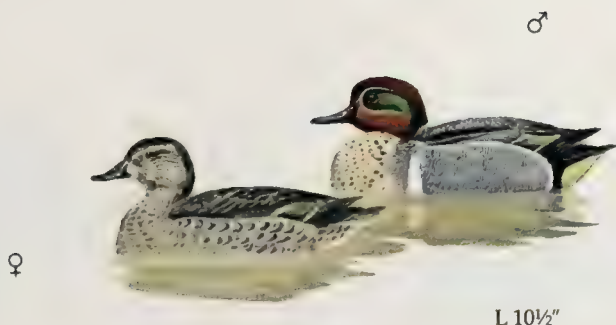
NEST: Prefers to nest in natural cavities 20 to 50 feet above ground with entrance holes of 4 inches in diameter, cavity depths of 2 feet, and cavity bottoms measuring 10 by 10 inches. Uses nest trees in (or up to one-half mile from) water 3 to 18 inches deep. Readily accepts nest boxes provided with nesting materials of wood shavings or sawdust.

FOOD: Eats about 90 percent plant material. Forages in ponds, marshes, sluggish streams, or along wooded banks for floating duckweeds, baldcypress cones and galls, seeds and tubers, wild rice, acorns, beechnuts, hickory nuts, grapes, berries, corn, and wheat. Also eats some invertebrates, such as spiders and aquatic insects.

REFERENCES: Bellrose 1976, Grice and Rogers 1965, McGilvrey 1968, Palmer 1976b, Terres 1980.

Green-winged Teal

Anas crecca



RANGE: Breeds from Alaska, northwestern and southern Mackenzie to north-central Labrador and Newfoundland south to central Oregon, Colorado, southern Ontario and Quebec, and Nova Scotia; Breeds locally from southern California east to southern New Mexico, Iowa, and Pennsylvania, and on the Atlantic Coast to Delaware. Winters from southern Alaska and southern British Columbia to New Brunswick and Nova Scotia south to Central America; also winters in the Hawaiian Islands.

STATUS: Relatively common throughout range.

HABITAT: Inhabits inland waters with dense rushes or other emergent vegetation on mixed and shortgrass prairies, and northern boreal forests. May be found resting on mudbanks or stumps, or perching on low limbs of dead trees. Winters in both freshwater and brackish marshes, ponds, streams, and estuaries.

SPECIAL HABITAT REQUIREMENTS: Lakes, marshes, ponds, pools, and shallow streams.

NEST: Nests in a depression on dry ground located at the base of shrubs, under a log, or in dense grass, usually 2 to 300 feet (but up to one-quarter mile) from water.

FOOD: Feeds in shallow marshes or temporarily flooded fields by dabbling, or by probing on mud flats. Consumes a diet that is about 90 percent vegetative, consisting of seeds of aquatic plants, grains, berries, wild grapes, mast, and (to a lesser extent) the vegetative parts of aquatic plants. Also eats some insects, small mollusks, and crustaceans.

REFERENCES: Bellrose 1976, Harrison 1975, Palmer 1976a, Terres 1980.

American Black Duck

Anas rubripes
(formerly Black Duck)



RANGE: Breeds from northern Saskatchewan to Labrador and Newfoundland south to northern South Dakota, northern Illinois, central West Virginia, and on the Atlantic Coast to North Carolina. Winters from southeastern Minnesota and central Wisconsin to New Brunswick and Nova Scotia south to southern Texas, the Gulf Coast and south-central Florida. Winters as far north as open water and food are available.

STATUS: Common, but the population is declining.

HABITAT: Inhabits a wide variety of wetland habitats along the coast and in woodlands, including open boreal forests and mixed hardwoods; sometimes is found in stubble fields or berry barrens. Generally is extremely adaptable as long as there is some source of water. Prefers to winter on brackish marshes bordering bays, estuaries, and agricultural lands but may also be found on lakes, reservoirs, rivers, freshwater marshes, and old rice fields.

NEST: Generally nests in a hollow on dry, slightly elevated ground in wooded areas, well-concealed in thickets, briars, shrubs or grasses, usually near (but possibly a mile or more from) water. Occasionally uses old crow or hawk nests and natural or excavated cavities in trees or tops of rotted stumps.

FOOD: Forages by dabbling in shallow water, and by gleaning and grazing in fields. Has a diet that varies widely, depending on habitat. In fresh and brackish areas eats mostly plants; in marine environments eats mostly animals. Consumes primarily blue mussels, submerged aquatic plants, waste grains, acorns, seeds of marsh plants, crustaceans, earthworms, amphibians, and fishes.

REFERENCES: Bellrose 1976, Benson 1968, Coulter and Mendall 1968, DeGraff et al. 1980, Johnsard 1975b, Palmer 1976a.

Mottled Duck

Anas fulvigula



RANGE: Breeds along the Gulf Coast from southern Louisiana and Texas into Mexico; in peninsular Florida; and locally inland in southeastern Colorado, western Kansas, Oklahoma, and northeastern Texas. Winters in the breeding range and casually along the entire Gulf Coast into Mexico. In Florida, does not migrate.

STATUS: Locally common.

HABITAT: Primarily inhabits extensive coastal marshes with a good interspersed of ponds but is also found in rice fields and on ponds and stream banks in pasture and farmlands. In Florida, inhabits ponds and lakes of pine flatwoods, everglades, cultivated and fallow fields, fresh and brackish marshes, mangrove swamps, and baldcypress-watertupelo hummocks.

SPECIAL HABITAT REQUIREMENTS: Freshwater and marine wetlands.

NEST: Builds a nest that is usually well concealed in a clump of grass, or on the ground under a bush, in meadows, generally within 500 feet of water. Prefers to nest near coastal marshes, but will also nest near ponds, bayous, or ditches. Is shy and sensitive to human disturbance.

FOOD: Feeds heavily on animal foods such as fish, crayfish, snails, and insects; also eats seeds of millet, rice, grasses, and aquatic plants.

REFERENCES: Beckwith and Hosford 1957, Bellrose 1976, Sincock et al. 1964, Singleton 1968.

Mallard

Anas platyrhynchos
(includes Mexican Duck)



RANGE: Breeds from northern Alaska east to southern Keewatin and across to southern Maine south to California, the southern Great Basin and New Mexico, and from Oklahoma east through the Ohio Valley to Virginia. Winters generally from southern Alaska and southern Canada south to central Mexico. Introduced and established in the Hawaiian Islands.

STATUS: The most common and widely distributed duck in North America.

HABITAT: Inhabits ponds, lakes, rivers, streams, marshes, wet meadows, and wooded swamps of primarily mixed and shortgrass prairie; also inhabits boreal forest region and sub-arctic deltas. Winters on inland ponds and rivers with some open water; less commonly in coastal marshes.

NEST: Typically nests on the ground in dry or slightly marshy areas within 300 feet of water, sometimes as far as 1.5 miles away in grasslands. Conceals nest well in snowberry clumps, among weeds and grasses, in pastures, stubble, or cultivated fields, or in marsh vegetation; rarely in cavities, on hollowed tops of stubs, or in tree crotches.

FOOD: Feeds by dabbling in shallow waters of ponds, sloughs, lakes, streams, and swamps, and by grazing and gleaning in grainfields and meadows. Consumes seeds, acorns, nuts, waste grains, aquatic insects, mollusks, tadpoles, frogs, small fish, and fish eggs.

REFERENCES: Bellrose 1976, DeGraff et al. 1980, Johnsgard 1975b, Palmer 1976a, Terres 1980.

Northern Pintail

Anas acuta

(formerly Pintail)



RANGE: Breeds from northern Alaska across northern Canada to northern and eastern Quebec, New Brunswick, and Nova Scotia to California, across to the Great Lakes, St. Lawrence River, and Maine. Winters from southern Alaska south to northern New Mexico, and east to central Missouri and the Ohio Valley (uncommonly); along the Atlantic Coast from Massachusetts, south throughout the southern United States to South America.

STATUS: Abundant in the West and common in the East.

HABITAT: Found in a wide variety of habitats, but typically inhabits open country with low vegetation and with many scattered small, shallow bodies of water. Frequents lakes, rivers, marshes and ponds in grasslands, barrens, dry tundra, open boreal forest, and cultivated fields. Winters on freshwater and brackish coastal marshes, shallow lagoons, mudflats along rivers, and sheltered marine waters.

SPECIAL HABITAT REQUIREMENTS: Drakes need mudbanks or exposed water margins for resting; also shallow wetlands for feeding.

NEST: Often builds a nest in a hollow on dry ground, sometimes concealed by grasses or shrubs, usually within 300 feet (occasionally a half mile) from water. Nests in stubble fields, in a dry portion within a large marsh, or in lightly grazed pasture, but generally avoids timbered or extensively brushy areas.

FOOD: Prefers to feed in shallow waters of marshes, ponds, and wet meadows, or in grainfields. Primarily a seed-eater; mostly (87 percent) consumes vegetative diet, consisting of seeds of pondweeds, sedges, grasses, smartweeds, and cultivated grains; also takes some fairy shrimp, snails, earthworms, mollusks, crustaceans, dipteran larvae, and other insects.

REFERENCES: Bellrose 1976, DeGraff et al. 1980, Johnsgard 1975b, Krapu 1974, Palmer 1976a.

Blue-winged Teal

Anas discors



RANGE: Breeds from east-central Alaska and southern Mackenzie to southern Quebec and southwestern Newfoundland, south to northeastern California, east across to central Louisiana, central Tennessee and eastern North Carolina. Winters from southern California to western and southern Texas, the Gulf Coast and North Carolina on the Atlantic Coast south to South America.

STATUS: Common throughout range.

HABITAT: Prefers wetlands on rolling tallgrass prairie but is also found in mixed shortgrass prairie and boreal and deciduous forests. More of a shoreline inhabitant than one of open water, prefers calm water or sluggish currents to fast water. Uses rocks protruding above water, muskrat houses, trunks or limbs of fallen trees, or bare stretches of shoreline or mudflats as resting sites. Winters on shallow inland freshwater marshes and on brackish and saltwater marshes.

SPECIAL HABITAT REQUIREMENTS: Marshes, sloughs, ponds, lakes, and sluggish streams.

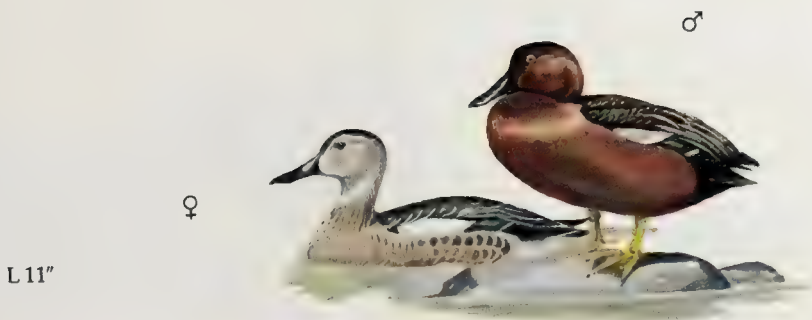
NEST: Builds nests on dry ground in dense grassy sites such as bluegrass, hayfields, and sedge meadows, where the vegetation ranges from 8 to 24 inches high at the onset of nesting, or under bushes, usually within several hundred yards of open water; occasionally on a sedge tussock or muskrat house, in slough grass, or in alfalfa fields. In good habitat nests communally.

FOOD: Prefers to feed on mud flats, in fields, or in shallow water where there is floating and shallowly submerged vegetation plus abundant small aquatic animal life. Consumes a diet that is 70 percent vegetative, consisting of seeds of sedges; grasses, pondweeds, and smartweeds; stems and leaves of aquatic plants; and snails, mollusks, crustaceans, and insects.

REFERENCES: Bellrose 1976, Bennet 1938, DeGraff et al. 1980, Johnsgard 1975b, Palmer 1976a.

Cinnamon Teal

Anas cyanoptera



RANGE: Breeds from southern British Columbia east to southwestern Saskatchewan (probably), and south into Mexico. Winters from central California, southern Nevada, central Utah, southeastern Arizona, southern New Mexico and central Texas south to South America.

STATUS: Common in the West.

HABITAT: Inhabits small, shallow wetlands, including areas with alkaline waters, but may also be found around larger and deeper lakes. Winters primarily on freshwaters, though occasionally found in marine habitats.

SPECIAL HABITAT REQUIREMENTS: Shallow lake margins, ponds bordered by tule and grasses, sloughs, marshes, sluggish streams, reservoirs, and irrigation ditches.

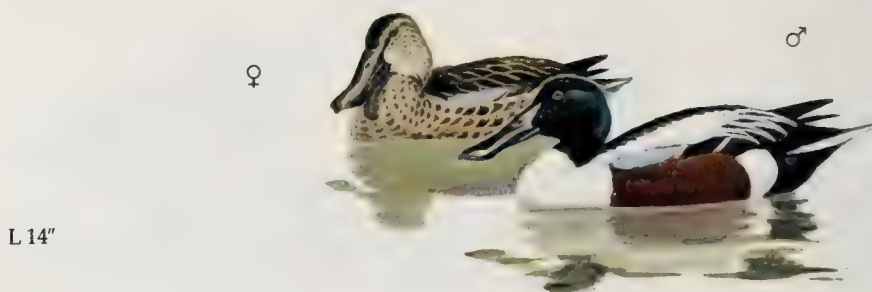
NEST: Nests on the ground in dense grasses under 2 feet high, in cattails or reeds near water, or in a hollow in the ground, often 100 feet or more from water. Broods may be moved as far as a mile from the nest site to good brood cover of lush emergent vegetation adjacent to water with abundant food.

FOOD: Feeds by tipping up in shallow water, grazes in grass and in fields, or probes in mud for its food, which is 80 percent vegetative. Primarily consumes seeds and vegetative parts of pondweeds, bulrushes, sedges, smartweeds and grasses; also takes mollusks and insects.

REFERENCES: Bellrose 1976, Grinnell and Miller 1944, Johnsgard 1975b, Low and Mansell 1983, Palmer 1976a, Verner and Boss 1980.

Northern Shoveler

Anas clypeata



L 14"

RANGE: Breeds from northern Alaska to northern Manitoba, south to northwestern and eastern Oregon, northern Utah, Colorado, Nebraska, and Missouri, and central Wisconsin. Winters from the coast of southern British Columbia to central Arizona east to the Gulf Coast and South Carolina on the Atlantic Coast south to South America.

STATUS: Fairly common; more abundant west of the Mississippi River.

HABITAT: Prefers shallow prairie marshes, particularly those with abundant plant and animal life floating on the surface, but also occupies potholes, sloughs, and marshes in taiga, forests, and (less commonly) cultivated country. It tolerates a wide range of water conditions, from clean and clear to muddy; flowing to stagnant; considerably alkaline, and even heavily polluted. Likes to have mudbanks or low sloping shorelines with short or flattened vegetation for loafing. Winters in freshwater and brackish habitats.

SPECIAL HABITAT REQUIREMENTS: Shallow waters with muddy bottoms, surrounded by dry grassy areas for nesting.

NEST: Nests on dry ground in a slight hollow, preferably in short grasses within 300 feet of water, but will nest in hayfields, meadows, and rarely bulrushes if grasses are not available. Seldom nests in weed patches, and avoids woody vegetation such as willows.

FOOD: A filter feeder; prefers to feed in shallow waters, but will actively feed in deep waters containing submergent and surface vegetation. Consumes a considerable amount of microscopic animal life such as ostracods, copepods, and similar crustaceans, and macroscopic animal life as well. Eats fingernail clams, mollusks, and insects for one quarter of the diet. Also eats grasses, sedges, water lilies, pondweeds, bulrush seeds, algae, and smartweeds.

REFERENCES: Bellrose 1976, DeGraff et al. 1980, Johnsgard 1975b, Palmer 1976a, Poston 1974.

Gadwall

Anas strepera



RANGE: Breeds from southern Alaska and southern Yukon to the New Brunswick-Nova Scotia border, south locally to southern California, northern Texas, central Minnesota, and northern Pennsylvania and on the Atlantic Coast to North Carolina. Winters from southern Alaska, southern British Columbia and Colorado to southern South Dakota, Iowa, the southern Great Lakes and Chesapeake Bay on the Atlantic Coast south to Mexico and the Gulf Coast.

STATUS: Uncommon, but numbers have increased substantially during the past 2 decades and the range is extending eastward.

HABITAT: Inhabits prairie marshes, sloughs, ponds or small lakes in grasslands in both freshwater and brackish habitats. Generally avoids wetlands bordered by woodlands or thick brush, preferring those bordered by dense, low herbaceous vegetation or shrubby willows and with grassy islands. Prefers to winter in freshwater, marshy habitats but can be found on open water of any kind.

SPECIAL HABITAT REQUIREMENTS: Shallow water for feeding; marshes or grassy areas near water for nesting.

NEST: Nests on the ground on a well-drained site on islands in lakes, in upland meadows or pastures, in alfalfa fields, or on prairies, usually within 150 feet of water. Prefers to nest in uplands rather than over water, especially in dense, coarse herbaceous vegetation and under shrubby willows.

FOOD: Prefers to feed along shallow marsh edges with abundant aquatic plant life, but also feeds in open water more than other dabblers. Sometimes feeds in stubble fields for grain, or in woods for acorns. Consumes mainly leaves and stems of aquatic plants; also eats insects, mollusks, crustaceans, amphibians, and fishes.

REFERENCES: Bellrose 1976, DeGraff et al. 1980, Johnsgard 1975b, Palmer 1976a, Terres 1980.

American Wigeon

Anas americana



RANGE: Breeds from central Alaska and central Yukon to New Brunswick and southern Nova Scotia, south to northeastern California, central Colorado, South Dakota, southern Ontario, and northern New York, sporadically to the Atlantic Coast. Winters from southern Alaska to southern Nevada, sporadically across the central United States to the southern Great Lakes and Ohio Valley, and on the Atlantic Coast from Nova Scotia south throughout the southern United States to Central America.

STATUS: Common.

HABITAT: Inhabits freshwater wetlands and lakes from tundra to shortgrass and mixed prairie, preferring permanent to temporary waters. Commonly associates with diving ducks, and in winter frequents coastal marshes and bays, wet meadows, and shallow freshwater and brackish ponds.

SPECIAL HABITAT REQUIREMENTS: Large lakes, ponds, marshes, sluggish streams and rivers, with open water and exposed shoreline.

NEST: Nests in a hollow on dry ground on an island or on shore, in tall grasses or weeds, or at the base of a tree or bush, as far as 400 yards from water.

FOOD: Feeds by grazing and gleaning in wet or dry pastures and fields, by dabbling on the water surface in shallow water along marsh edges and sloughs, and by scavenging for wild celery after diving ducks have torn plants loose from bottom. Primarily vegetarian, eats mainly leaves, stems, and buds of aquatic plants; also feeds on waste grains, mollusks, crustaceans, and insects.

REFERENCES: Baldwin et al. 1964, Bellrose 1976, DeGraff et al. 1980, Johnsgard 1975b, Low and Mansell 1983, Palmer 1976a, Terres 1980, Verner and Boss 1980.

Canvasback

Aythya valisineria



RANGE: Breeds from central Alaska and northern Yukon to western Ontario and south to south-coastal Alaska; locally in inland areas to northeastern California across to northern Utah, central New Mexico, northwestern Iowa, and southern Ontario. Winters along the Pacific Coast from the central Aleutians and south-coastal Alaska south to Baja California, from Arizona and New Mexico to the Great Lakes, and, on the Atlantic Coast, from New England south to the Gulf Coast and Mexico.

STATUS: Locally common; numbers are declining due to loss of breeding habitat through drainage and drought.

HABITAT: Prefers shallow prairie marshes, 10 acres or less, or other permanent wetlands with stable water levels, bordered by cattails and bulrushes, with little, if any, wooded vegetation around the shoreline. Large lakes of 150 acres or more, marshes, and rivers with submerged beds of sago pondweed are favored during migration. Winters primarily on estuaries and sheltered bays, sometimes on deep, freshwater lakes, where wild celery and pondweeds thrive.

SPECIAL HABITAT REQUIREMENTS: Marshes, ponds, lakes, and rivers bordered by emergent vegetation and with enough open water for taking off and landing.

NEST: Usually nests over water 6 to 24 inches deep in bulrushes, reeds, or cattails, sometimes on a muskrat house, rarely on dry ground. Attaches nest to surrounding plants or built on a mat of floating dead plants, 3 to 60 feet from edge of open water.

FOOD: Dives in shallow water, usually 3 to 12 feet deep, for food, which is 80 percent vegetative material. In the Northeast, prefers seeds and vegetative parts of wild celery; in the Southeast and the West, primarily consumes pondweeds; also feeds on water plantains, grasses, sedges, mollusks, and insects.

REFERENCES: Bellrose 1976, DeGraff et al. 1980, Evans and Bartels 1981, Johnsgard 1975b, Palmer 1976b, Stoudt 1982, Terres 1980.

Redhead

Aythya americana



RANGE: Breeds from central British Columbia and southwestern Mackenzie to northwestern and central Minnesota, south to southern California, the Texas Panhandle and northern Iowa; locally in south-central and southeastern Alaska, and sporadically in eastern North America. Winters from British Columbia on the Pacific Coast, in the interior from Nevada to the middle Mississippi and Ohio Valleys and the Great Lakes, and from New England on the Atlantic Coast south throughout the southern United States to Mexico.

STATUS: Common; population declining in the eastern United States.

HABITAT: Inhabits freshwater marshes, sloughs, ponds, and shallow lakes bordered by hardstem bulrush, cattails, reeds, or sedges in prairies and intermountain parks. Winters primarily on freshwater and brackish lakes, rivers, and estuaries, in areas well protected from heavy wave action.

SPECIAL HABITAT REQUIREMENTS: Wetlands at least 1/2 acre in size bordered by permanent, dense emergent vegetation, with stable water levels during the nesting season.

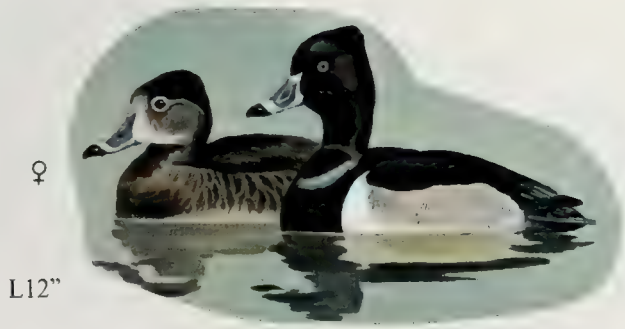
NEST: Usually nests in emergent vegetation or on a floating mat of dead plant material over shallow water 6 to 14 inches deep, fairly close to shore, but occasionally on dry ground or over water 4 feet deep. Tends to be semi-parasitic, sometimes laying eggs in nests of other waterfowl, especially the canvasback; also incubates own nests. Prefers to rear broods in potholes at least 1 acre in size, with deeper waters than those used for nesting.

FOOD: Feeds in marshes, sloughs, and ponds more than other diving ducks, mainly in water less than 6 feet deep. Has a diet that is 90 percent vegetative, consisting primarily of seeds and vegetative parts of aquatic plants and including some insects and shellfish.

REFERENCES: Bellrose 1976, DeGraff et al. 1980, Johnsard 1975b, Lokemoen 1966, Palmer 1976b, Tate and Tate 1982, Weller 1964.

Ring-necked Duck

Aythya collaris



RANGE: Breeds in east-central and southeastern Alaska, and from central British Columbia and northwestern and southern Mackenzie to Newfoundland and Nova Scotia, south to northeastern California, southeastern Arizona, northern Illinois, and Massachusetts. Winters on the Pacific Coast from southeastern Alaska, in the interior from southern Nevada to the lower Mississippi and Ohio Valleys, and on the Atlantic Coast from New England south through the southern United States to Panama.

STATUS: Common.

HABITAT: Inhabits shallow, dense bogs, swamps, and marshes, especially those with sweetgale or leatherleaf cover, from 1 to 2,000 acres in size, typically having a pH range of 5.5 to 6.8, and preferably near or in woodlands. It also uses small potholes, sloughs, and beaver flowages near larger wooded lakes or rivers with submerged and emergent vegetation. Winters on fresh or brackish marshes, lakes, and estuaries, rarely on strictly saline waters.

SPECIAL HABITAT REQUIREMENTS: Wetlands with an expanse of open water.

NEST: Nests on floating mats of vegetation, among hummocks, in clumps of marsh vegetation or on islands, on relatively dry sites usually within a few feet of water; seldom in emergent vegetation over water.

FOOD: Prefers to feed in shallow water, usually less than 6 feet deep. Consumes a diet that is 80 percent vegetative, consisting mostly of a few plant groups; seeds, bulbs, and succulent parts of waterlilies, pondweeds, sedges, grasses, and smartweeds. Also consumes some aquatic insects and mollusks.

REFERENCES: Bellrose 1976, DeGraff et al. 1980, Johnsgard 1975b, Mendall 1958, Palmer 1976b.

Greater Scaup

Aythya marila



RANGE: Breeds from western Alaska to southern Keewatin, around Hudson and James Bays, and northern Quebec; casually or irregularly south to southeastern Alaska, northwestern British Columbia, central Manitoba, and southeastern Michigan. Winters along the Pacific Coast from the Aleutians and southeastern Alaska south to Baja California, in the eastern Great Lakes, from the Ohio and lower Mississippi Valleys south to the Gulf Coast, and on the Atlantic Coast from Newfoundland south to Florida.

STATUS: Locally common.

HABITAT: Inhabits lakes, ponds, and marshes from forested tundra to richly vegetated low tundra. During the breeding season, drakes rest along shorelines or on shoals, while in late fall and winter, both sexes form large rafts in open water, even in the open ocean well beyond the breakers. Winters on brackish and saltwater bays and estuaries, less commonly on large inland waters.

SPECIAL HABITAT REQUIREMENTS: Scattered wetlands in forested to open tundra.

NEST: Nests on the ground in a slightly elevated spot, in grasses on the tundra, usually near the shores of lakes or ponds, but up to 3,000 feet from water. Sometimes nests on islands, in marshes, or above or in water among rushes or wild rice.

FOOD: An expert diver; dives to depths of at least 20 feet, remaining underwater seeking food for up to a minute. A saltwater bird most of the year; prefers to feed in shoals with water less than 20 feet deep or in shellfish beds, also in freshwater lakes and ponds. Consumes a diet that is about half vegetative and half animal, including snails, aquatic insects, tadpoles, small fishes, and seeds in summer. During winter, also eats mollusks, crabs, barnacles, and other crustaceans. Also feeds on muskgrass, sea lettuce, eelgrass, wild celery, and widgeon grass.

REFERENCES: Cottam 1939, Johnsgard 1975b, Palmer 1976b, Terres 1980, Vickery in Farrand 1983a.

Lesser Scaup

Aythya affinis



RANGE: Breeds from central Alaska to northern Manitoba and western Ontario, south to southern interior British Columbia, northern Wyoming and northwestern and central Minnesota; casually or irregularly east to southern Ontario and west-central Quebec, and south to northeastern California and Colorado, northern Illinois and northern Ohio. Winters from southern Alaska and southern British Columbia and Utah to the southern Great Lakes Region and New England, south throughout the southern United States to South America.

STATUS: Abundant.

HABITAT: Inhabits grass-margined wetlands in prairie and forested habitats, with the largest breeding concentrations found in marshes of hardstem bulrush bordering lakes. Winters on sheltered bays, estuaries, coastal marshes, and freshwater lakes, preferring a more sheltered habitat than the greater scaup.

SPECIAL HABITAT REQUIREMENTS: Lakes, ponds, potholes, marshes, and sloughs bordered by grasses.

NEST: Usually nests in upland areas adjacent to water but also on islands, in wet meadows, in shallows at edges of bays and sloughs among bulrushes or on tussocks in marshes. Conceals nest well in hollows on usually dry ground, in grasses, nettles, low brush, even under driftwood.

FOOD: An expert diver, generally feeds in water 5 to 6 feet deep, but may feed to depths of 15 to 20 feet. Consumes plant and animal foods about equally, including seeds and vegetative parts of pondweeds, grasses, sedges, widgeon grass, wild rice, bulrushes, snails and other mollusks, crustaceans, and aquatic insects.

REFERENCES: Bellrose 1976, Johnsgard 1975b, Palmer 1976b, Terres 1980.

Harlequin Duck

Histrionicus histrionicus



RANGE: Breeds in western North America from western Alaska and northern Yukon south to Vancouver Island, eastern Oregon and western Wyoming; in the Sierra Nevada of California, and in eastern North America from southern Baffin Island south to central and eastern Quebec and eastern Labrador. Winters along the Pacific Coast from the Pribilof and Aleutian Islands south to central California; on the Atlantic Coast from southern Labrador south to New York (rarely to South Carolina); casually farther inland south to Kansas and West Virginia and Florida.

STATUS: Uncommon to locally abundant.

HABITAT: Prefers cold, shallow, rapidly flowing mountain streams in forested regions, but also inhabits ponds and lakes, along rocky Arctic shores, and in tundra. Loafs in shallows, or on a rock or log in a stream or ashore. Winters on marine waters, usually 6 to 12 feet deep, in heavy surf along rocky coasts.

SPECIAL HABITAT REQUIREMENTS: Shallow, swift streams or rivers, or pothole glacial lakes.

NEST: Nests on the ground on an island, in a recess in a stream bank, under bushes or trees, or occasionally in a hollow tree or a cavity among rocks. Usually nests within 6 feet (but sometimes up to 60 feet) from water, with overhead shelter.

FOOD: A proficient diver, seems to prefer to feed in rough waters broken by rocks and surf. Mostly (98 percent) consumes crustaceans and mollusks. Also eats stone flies and other insects, fishes, and echinoderms.

REFERENCES: Bellrose 1976, Cottam 1939, Johnsgard 1975b, Palmer 1976b, Terres 1980.

White-winged Scoter

Melanitta fusca



RANGE: Breeds from northern Alaska to southern Keewatin and northern Manitoba south to central Alaska, northeastern Washington, southern Saskatchewan, northern North Dakota and northern Ontario; possibly farther east. Winters on the Pacific Coast from the Aleutians south to Baja California, on the Great Lakes, and on the Atlantic Coast from Newfoundland south to South Carolina.

STATUS: Common to locally abundant.

HABITAT: Inhabits waters on open tundra or prairie with dense, low ground cover, preferably lakes larger than 110 acres, 3 to 12 feet deep and with dense submergent vegetation. Uses mixed tundra-taiga less frequently during nesting. In other seasons, can be found on marine and brackish waters along the coasts where the water is shallow over shellfish beds and the bottom is hard and sandy or gravelly, and occasionally on open freshwater.

SPECIAL HABITAT REQUIREMENTS: Lakes, ponds, and sluggish streams in northern prairie or tundra.

NEST: Nests in a hollow on the ground under dense, low spreading shrubs, preferably gooseberry, snowberry, rose, and raspberry, usually close to water, occasionally up to 450 feet and rarely a half mile away. May nest on islands, commonly uses old nest bowls, and in some instances may occupy active blue-winged teal or gadwall nests. Easily disturbed by human interference such as recreational boating on breeding lakes. Broods are reared in shallow, open water areas with submergent vegetation and some protection from wave action.

FOOD: Prefers to dive for shellfish in shallow water, usually less than 6 feet deep. Primarily eats animal foods (90 percent), mostly mollusks; also eats crabs, some fishes, aquatic insects, and sea lettuce.

REFERENCES: Brown and Brown 1981, Grosz and Yocom 1972, Palmer 1976b.

Common Goldeneye

Bucephala clangula



RANGE: Breeds from western Alaska and northern Yukon to central Labrador and Newfoundland, south to central Alaska, northern Washington across to northern Michigan, Maine, New Brunswick, and Nova Scotia. Winters on the Pacific Coast from the Aleutian Islands south to southern California, on the Great Lakes, in the Mississippi and Ohio Valleys, and south to the Gulf Coast, and on the Atlantic Coast from Newfoundland south to Florida; irregularly elsewhere in the interior of the United States.

STATUS: Common.

HABITAT: Inhabits lakes, ponds, shallow rivers, slow-flowing streams, floodplain forests and bogs, preferably with weedy margins, near or in woodlands with large cavity trees. Breeds in a range that generally coincides with the boreal coniferous forest. Winters on bays, estuaries, rivers, and inland as far north as open water and food are available.

SPECIAL HABITAT REQUIREMENTS: Large trees (minimum dbh of 20 inches) with cavities for nesting, near clear, cold, shallow water for feeding.

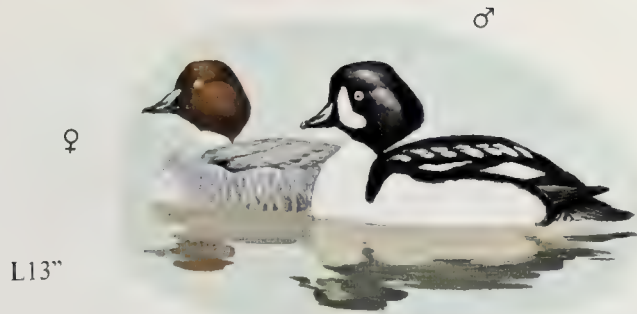
NEST: Nests in tree cavities near or in water, preferably open-top, bucket cavities, but also in old pileated woodpecker cavities, in hollow stumps, in natural cavities, or when cavities are not available, in abandoned buildings, cavities among rocks, and nest boxes. Sometimes may lay joint clutches when cavities are scarce. Prefers nest tree entrances that are 6 to 40 feet above ground or water. Accepts nest boxes that are 9 by 9 by 24 inches in size, with an elliptical entrance 3 1/2 by 4 1/2 inches.

FOOD: Prefers to dive for food in water 3 to 12 feet deep. Consumes animal food, as 75 percent of the diet, including crabs, crayfish, mussels, snails, insects, and some fishes. Also eats seeds, tubers, and leafy parts of pondweeds; seeds of pond lilies and bulrushes; and wild celery.

REFERENCES: Carter 1958, Cottam 1939, DeGraff et al. 1980, Johnsgard 1975b, Palmer 1976b, Thomas et al. 1979.

Barrow's Goldeneye

Bucephala islandica



RANGE: Breeds from central and southwestern Alaska, southern Yukon and southwestern Alberta south to south-coastal and southeastern Alaska, southern British Columbia, and northern Washington; locally at higher elevations to northwestern Wyoming, and in northeastern Quebec and northern Labrador. Winters along the Pacific Coast from south-coastal and southeastern Alaska south to central California; locally in the interior of western North America; and in the Atlantic region from the upper St. Lawrence drainage and Nova Scotia south to New York, rarely to South Carolina.

STATUS: Uncommon.

HABITAT: Inhabits lakes and ponds larger than 2 acres in montane, tundra, and subundra habitats. Prefers moderately alkaline lakes, 5 to 15 feet deep, with a dense growth of submerged aquatic vegetation such as pondweeds and widgeon grass, and bordered by dense stands of bulrushes. Winters on lakes and rivers, and in coastal estuaries and bays where rocky reefs and ledges in shallow water provide feeding grounds.

SPECIAL HABITAT REQUIREMENTS: Cavities in trees near open water.

NEST: Nests in natural cavities in trees and stumps, in abandoned flicker nest cavities enlarged by natural decay, pileated woodpecker holes, or nest boxes, preferably within 100 feet of water. Occasionally may nest up to a half mile from water. Nests in dead or dying Douglas-fir, aspen, cottonwoods, lodgepole pine, ponderosa pine, and less commonly scrub pine. If tree cavities are not available, nests in holes in the ground or in cavities in rock cliffs or under rocks.

FOOD: Dives and forages in open water to depths of 3 to 10 feet for its food, which is 78 percent animal material. Primarily consumes insect nymphs and larvae, and water boatmen; crustaceans, especially crayfish; and some fishes, blue mussels, pondweeds, and wild celery.

REFERENCES: Cottam 1939, Bellrose 1976, Johnsgard 1975b, Palmer 1976b, Terres 1980.

Bufflehead

Bucephala albeola



RANGE: Breeds from central Alaska to northeastern Manitoba and northern Ontario south to northern Washington, southern Manitoba and locally in southern Ontario; also locally south to the mountains of northern California, and to Wyoming, Iowa, and Wisconsin. Winters from the Aleutian Islands on the Pacific Coast, the Great Lakes, and Newfoundland on the Atlantic, south in coastal states and the Ohio and Mississippi Valleys to the southern United States and Mexico.

STATUS: Common.

HABITAT: Primarily inhabits small, shallow, fresh or slightly alkaline lakes and ponds, preferably without broad margins of emergent or floating aquatic vegetation, in mixed coniferous-deciduous woodlands north and west of the Great Plains. Logs, stumps, rocks, open shore, and sometimes fence rails near water are used for resting and loafing. Winters in sheltered marine habitats, or on brackish or freshwater.

SPECIAL HABITAT REQUIREMENTS: Tree cavities excavated by woodpeckers, especially northern flickers, near shallow, fertile waters in forested regions.

NEST: Prefers to nest in aspen trees near water containing unaltered northern flicker holes, but will also use pileated woodpecker holes. Also nests in Douglas-fir, balsam poplar, black cottonwood, ponderosa pine, and a few other coniferous and deciduous trees. Nests generally within 75 feet of water and rarely in dense forest. In some areas, accepts nest boxes 7 inches in diameter and 16 inches deep with entrances 2 7/8 inches wide.

FOOD: Prefers to forage in shallow water, diving to depths of 6 to 10 feet for food which is primarily animal material. In summer, mostly eats aquatic insects and larvae, but also includes water boatmen, shrimplike amphipods, some snails and small fishes, and seeds of pondweeds and naiads. During winter, mostly eats shrimp, snails, and other crustaceans.

REFERENCES: Erskine 1971, Johnsgard 1975b, Palmer 1976b, Terres 1980.

Hooded Merganser

Lophodytes cucullatus



RANGE: Breeds from southern Alaska to Nova Scotia, south to Oregon and Idaho, east to Maine and Massachusetts, and locally in the Mississippi Valley and southeastern United States. Winters on freshwater from British Columbia and New England south to California, Texas, Florida, and northern Mexico.

STATUS: Locally common or rare.

HABITAT: Inhabits wooded, clear freshwater habitats, preferably water with sandy, gravelly, or cobbled bottoms. Prefers fast-flowing water, but also uses standing water as long as it is clear, small fish and invertebrates are abundant, and nest sites are available. Easily disturbed and thus tends to avoid areas of human activity. In Wisconsin, brood habitat was described as rivers with high levels of food resources, fast current velocities (0.80 to 0.93 feet/second), and wide (40 to 60 feet) and moderately deep (1 to 2 feet) channels with cobbled bottoms and heavy surrounding cover of mixed hardwoods.

SPECIAL HABITAT REQUIREMENTS: Wooded, clear water streams, rivers, swamps, ponds, and lakes with cavity trees.

NEST: A cavity nester that uses almost any hole or hollow tree, at any height, as long as it is large enough for the female and her nest. The nest tree is usually within a few yards of, or standing in, water. Prefers flooded shoreline with standing trees, and with snags or stumps interspersed but will nest in other locations, including nest boxes.

FOOD: Captures food during short dives in shallow, often rapidly flowing water, or at water surface. Eats small fishes (mainly rough fish), crayfish and other crustaceans, many aquatic insects such as caddis fly larvae and dragonfly nymphs, also some seeds and parts of aquatic plants.

REFERENCES: Bellrose 1976, Johnsgard 1975b, Kitchen and Hunt 1969, Morse et al. 1969, Palmer 1976b, Terres 1980, Vickery in Farrand 1983a.

Common Merganser

Mergus merganser



RANGE: Breeds in North America from central and south-coastal Alaska, northern Saskatchewan, and Newfoundland south to the mountains of central California and northern New Mexico. East of the Rockies, breeds south to southern Saskatchewan, central Michigan, southern Maine, and west-central Nova Scotia. Winters from the Aleutian Islands and south-coastal Alaska east across southern Canada to Newfoundland and south to southern California and the Gulf Coast from southern Texas to central Florida. Winters as far north as open inland waters are available.

STATUS: Common throughout range.

HABITAT: Prefers to breed in ponds associated with upper portions of rivers in forested regions, and clear, freshwater lakes with forested shorelines. Is transcontinental in character, but essentially confined to forested regions.

SPECIAL HABITAT REQUIREMENTS: Clear, forested streams, rivers, and lakes with tree cavities.

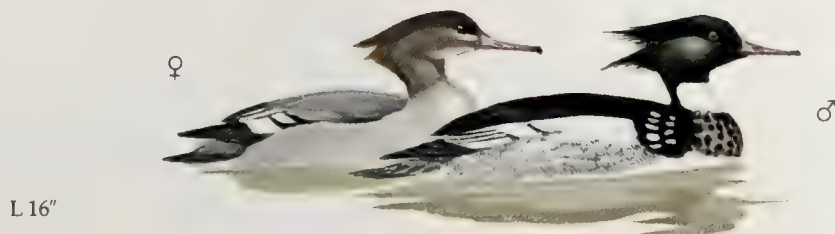
NEST: Generally nests in cavities in hollow trees near water, but also in dark recesses, on the ground, or in nest boxes. Height of tree cavity and species of tree are unimportant, but the number of suitable cavities available is definitely limited. May nest beneath boulders, in root tangles along undercut streambanks, in crevices in cliffs, or in chimneys, as long as the nest is concealed from above. One pair may use 2 to 3 miles of river during nesting.

FOOD: An opportunistic forager, generally feeds in fairly shallow waters from 1 1/2 to 6 feet deep. Consumes a wide variety of fishes, primarily rough and forage fish, but may be detrimental in areas specifically managed for trout or salmon production. Also eats frogs, aquatic salamanders, crayfish, shrimp, and other small crustaceans, snails and other mollusks, leeches, worms, aquatic insects and their larvae, and the roots and stems of aquatic plants.

REFERENCES: Bellrose 1976, Johnsgard 1975b, Palmer 1976b, Terres 1980, Timken and Anderson 1969.

Red-breasted Merganser

Mergus serrator



L 16"

RANGE: Breeds from northern Alaska to central Keewatin, northern Baffin Island, Labrador and Newfoundland south to the Aleutian Islands, northern British Columbia, central Minnesota, northern New York and Nova Scotia, casually south along the Atlantic Coast to Long Island. Winters primarily along coasts and on large inland bodies of water from southern Alaska, the Great Lakes and Nova Scotia south to Baja California, southern Texas, and the Gulf Coast.

STATUS: Common.

HABITAT: Prefers to breed on small islands or islets with low, prostrate woody vegetation or other natural features to cover the nest, and with open shores, gravel bars, or rocks to provide roosting and preening areas for drakes and young. Although it prefers inland waters, it may be found along the coasts on shores and on marine islets. Winters mainly in estuaries and sheltered bays, less frequently on inland freshwater.

SPECIAL HABITAT REQUIREMENTS: Rivers, ponds, and lakes with some overhead cover nearby for nesting.

NEST: Nests on the ground under low cover, generally within 33 feet of water, preferably on islands, but also on riverbanks and lakeshores, in marshes, on rocky islets, or in bank recesses. Nests may be under low conifer boughs; under or between boulders in shallow cavities; in tall grass, heather, or bracken; or under driftwood.

FOOD: Feeds primarily on fish caught during dives underwater. Also eats fish eggs, frogs, annelids, nymphs, caddis flies, amphipods, crabs, prawns, and mollusks.

REFERENCES: Bellrose 1976, Clapp et al. 1982, Johnsgard 1975b, Palmer 1976b.

Ruddy Duck

Oxyura jamaicensis



RANGE: Breeds in east-central Alaska and from central and northeastern British Columbia to western Ontario and south to southern California, western and southern Texas, and southwestern Louisiana, with some scattered breeding east to Nova Scotia and south to Florida. Winters from southern British Columbia, Idaho, Colorado, Kansas, the Great Lakes, and on the Atlantic Coast from Massachusetts south throughout the southern United States to Mexico.

STATUS: Common.

HABITAT: Inhabits permanent freshwater and alkaline prairie marshes having dense stands of cattails, bulrushes, whitetop, and reeds, and relatively stable water levels. Both large and small marshes are used for nesting, from potholes less than one acre to 1,200-acre sloughs. Commonly loafs and rests on water well out from shore. Prefers large bodies of shallow freshwater and brackish water, especially those with areas of aquatic plant growth, during migration. Winters on ice-free inland waters, or on sheltered shallow brackish or saltwater coastal waters.

SPECIAL HABITAT REQUIREMENTS: Open water areas close to dense emergent vegetation with muskrat channels or natural passageways to allow movement between the nest site and open water.

NEST: Usually nests over shallow water in emergent vegetation, on a floating mat of vegetation, or on a platform built up from the floor of the marsh. Occasionally nests on a muskrat house, on floating logs, or on an old coot nest. "Dump" nests are common in marshes with fluctuating water levels.

FOOD: Dives for food in waters 2 to 10 feet deep, and occasionally feeds on the water surface. Consumes about 72 percent plant foods, consisting of seeds, tubers, leaves, and algae. Also eats insects, snails, and some crustaceans.

REFERENCES: Bellrose 1976, Clapp et al. 1982, Cottam 1939, DeGraff et al. 1980, Johnsgard 1975b, Joyner 1969, Palmer 1976b, Siegfried 1976.

Black Vulture

Coragyps atratus



L 22" W 54"

RANGE: Resident from southern Arizona and western Texas to southern Illinois, southern Indiana and New Jersey south to the Gulf Coast, southern Florida, and South America. May retreat from northern range limits in winter.

STATUS: Common, but the population is declining in the southern Atlantic Coast region; range is extending slightly northward.

HABITAT: Nearly ubiquitous except in heavily forested regions. It is found in the southern Great Plains, southeastern pine forests, oak-hickory forests, and intermediate oak-pine forests.

NEST: Does not construct a nest. Frequently lays eggs in hollow bases of trees or stumps, rarely more than 10 to 15 feet above ground, but also on the ground, under dense or thorny vegetation, in cavities of rocks, on the floor of caves, on cliff ledges, or in abandoned buildings.

FOOD: Feeds primarily on carrion from city dumps, sewers, slaughterhouses, and roadkills along highways. Also kills and eats baby herons, domestic ducks, newborn calves, baby lambs, skunks, and opossums; feeds at times on ripe and rotten fruit and vegetables.

REFERENCES: Armistead in Farrand 1983a, Brown and Amadon 1968, Harrison 1979, Heintzelman 1979, Scott et al. 1977, Tate and Tate 1982, Terres 1980.

Turkey Vulture

Cathartes aura



L 25" W 72"

RANGE: Breeds from southern British Columbia, western Ontario, extreme southern Ontario and Massachusetts south throughout the remaining continental United States to South America. Winters from northern California, Arizona, Texas, Nebraska, the Ohio Valley, and Pennsylvania south to the Gulf Coast, Florida, and South America.

STATUS: Common.

HABITAT: Uses a wide variety of habitats, from the tropics and forested habitats dominated by mixed or deciduous trees to open plains and deserts, and from lowlands to mountains. Preens and roosts in tall snags or trees with open branches. May gather in groups of up to 70 birds to roost at night.

NEST: Does not build a nest. Lays eggs on the floor of caves (preferably one which has 2 entrances), on the ground inside dense shrubs, in hollow logs or stumps, on rocky outcrops or ledges, in swamps, in hollow snags, in old hawk nests, or on the floor in abandoned buildings. The eggs are usually well-hidden from view and inaccessible to predators.

FOOD: Feeds almost entirely on carrion in any state, from fresh to putrid, sighted while soaring over open fields, ridges, roads, or any type of clearing. Although partial to carrion of small mammals, amphibians, reptiles, birds, and fish, will consume carrion of large animals. Gathers quickly after the death of an animal to feed.

REFERENCES: Brown and Amadon 1968, DeGraff et al. 1980, Grinnell and Miller 1944, Heintzelman 1979, Sprunt 1955, Terres 1980.

California Condor

Gymnogyps californianus



L 45" W 120"

RANGE: Coastal ranges of California from Monterey and San Benito Counties south to Ventura County, ranging, at least casually, north to Santa Clara and San Mateo Counties, and east to the western slope of the Sierra Nevada and the Tehachapi Mountains, with breeding sites apparently confined to Los Padres National Forest in Santa Barbara, Ventura, and extreme northern Los Angeles Counties.

STATUS: Endangered. All known individuals are now in captivity.

HABITAT: Inhabited rugged canyons, gorges and forested mountains of southern California mainly between 985 and 8,860 feet in elevation; nested primarily between 2,000 to 4,500 feet in elevation. Spent a great deal of time roosting, preferably on dead conifers 40 to 70 feet tall, but also in live conifers and on cliffs. Needed a long, unobstructed space for taking off downhill from the roost site, which was located in areas protected from the wind, and near food, water, and nest sites.

SPECIAL HABITAT REQUIREMENTS: Tall conifers or cliffs for roosting, open grasslands for feeding, cliffs for nesting, and freedom from human disturbance.

NEST: Nesting areas were characterized by extremely steep, rugged terrain, with dense brush and groves of Douglas-fir surrounding high sandstone cliffs. Nested in a cavity in rock or among boulders on cliffs, with space enough to hold 2 full-grown condors, with perches available for both young and adults, protection from the elements, and space below for taking off.

FOOD: Fed in open grassland because of its need for space for taking flight. Sighted food while soaring over the countryside; 95 percent of diet was carcasses of cattle, sheep, ground squirrels, deer, and horses in any state of decay. Preferred to drink water from clear pools at the tops of waterfalls, but when pressed would obtain water from any source.

REFERENCES: Koford 1953, Mackenzie 1977, Wilbur 1978.

Osprey

Pandion haliaetus



L 22" W 54"

RANGE: Breeds from northwestern Alaska and northern Yukon to central Labrador and Newfoundland south locally to Baja California, central Arizona, southern Texas, the Gulf Coast, and southern Florida. Winters from central California, southern Texas, the Gulf Coast and Florida south to South America.

STATUS: Locally common to uncommon; population declining due to destruction of habitat, pesticides, human disturbance, and reduction of food resources.

HABITAT: Nearly cosmopolitan distribution, occurring on every continent except Antarctica. Occupies a wide range of habitats in association with water, primarily near lakes, rivers, and along coastal waters with adequate supplies of fish.

SPECIAL HABITAT REQUIREMENTS: Elevated nest sites near water with rich fish resources.

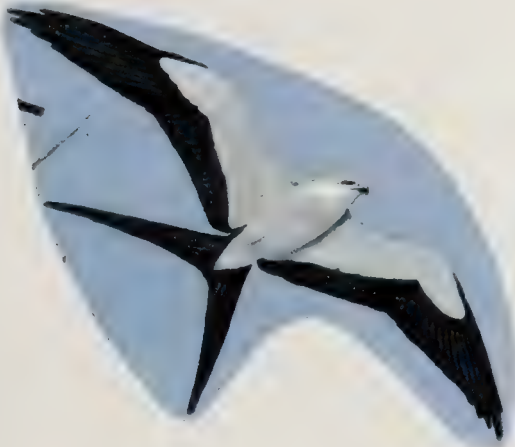
NEST: Nests in loose colonies or singly, and uses a wide variety of structures to support large stick nests, which may be 60 feet or more above ground. Prefers a snag in or near water, with a broken top or side limbs able to support the nest. Prefers tall snags that provide good visibility and security. Also nests on pilings, utility poles, duck blinds, buildings, steel towers for transmission lines, windmills, channel markers, fences, a wide variety of living, partially dead, or dead trees, wooden platforms in marshes, on cliffs, and sometimes on the ground. Nest site may be used by the same pair year after year.

FOOD: Feeds almost exclusively on fish; flies 50 to 100 feet above (preferably shallow) water, then hovers and plunges into the water to catch fish. Also eats frogs, snakes, ducks, crows, night-herons, and small mammals.

REFERENCES: DeGraff et al. 1980, Heintzelman 1979, Sprunt 1955, Zarn 1974a.

American Swallow-tailed Kite

Elanoides forficatus
(formerly Swallow-tailed Kite)



L21”

RANGE: Breeds locally from South Carolina south to Florida, and west to Louisiana; occasionally to Great Lakes and New England and also Central and South America. Winters in South America.

STATUS: Locally common.

HABITAT: Inhabits open river bottom forests with adjacent semi-prairie land, freshwater marshes bordering large lakes, lowland cypress swamps, and pine glades.

SPECIAL HABITAT REQUIREMENTS: Very tall living trees for nesting.

NEST: Nests in the very tops of tall, slender living trees, usually 60 to 100 feet above ground, but up to 200 feet high. In Florida, usually nests in pines or in black mangroves. Selects trees in open, thinly wooded areas, or along the edge of trails or openings so the birds can approach the nest unimpeded. Other kites are tolerated near the nest, but not other hawks or eagles.

FOOD: Feeds entirely on the wing, primarily on flying insects, but also sweeps low over fields, forest canopies, and prairies to catch grasshoppers, crickets, cicadas, small snakes, lizards, and frogs. Also snatches young birds and eggs, and drinks while skimming the surface of a lake or pond.

REFERENCES: Brown and Amadon 1968, Heintzelman 1979, Oberholser 1974a, Terres 1980.

Black-shouldered Kite

Elanus caeruleus
(formerly White-tailed Kite)



L14"

RANGE: Resident locally from northwestern Oregon south (west of the deserts) to Baja California, and from southern Oklahoma, western Louisiana, east-central and southeastern Texas south to South America. Strays to adjacent states, also to Florida, and in the Mississippi Valley north to Missouri and southern Illinois.

STATUS: Rare to locally fairly common; once reduced in numbers almost to the point of extinction in the United States. Year-round irrigation of agricultural land has improved habitat conditions in recent years.

HABITAT: Inhabits open country around freshwater marshes, moist meadows, alfalfa fields, and cultivated bottomlands, with scattered clumps of trees. In the western Sierra Nevada in California, found below 1,000 feet in blue oak-savannah, digger pine-oak, and riparian deciduous types.

SPECIAL HABITAT REQUIREMENTS: Trees with dense canopies for nesting near a permanent water source and an abundant population of voles (*Microtus* spp.).

NEST: Nests in oak, willow, eucalyptus, cottonwood, or other hardwood trees, from 18 to 59 feet above ground, usually near a marsh, streambank, or canal, and areas where voles are abundant. With good vole populations, breeding pairs need a minimum of 20 acres around the nest site for hunting.

FOOD: Searches for food by flying and hovering at less than 100 feet above ground. Feeds primarily on voles, but also eats other small mammals, small snakes, lizards, frogs, and large insects such as grasshoppers, beetles, and crickets.

REFERENCES: Brown and Amadon 1968, Heintzelman 1979, Oberholser 1974a, Terres 1980, Verner and Boss 1980.

Snail Kite

Rostrhamus sociabilis
(formerly Everglade Kite)



RANGE: Resident in southern Florida, primarily at Lake Okeechobee and Loxahatchee National Wildlife Refuge, and locally throughout the Everglades basin and the upper St. John's River.

STATUS: Endangered due to habitat destruction, hunting, and drought.

HABITAT: Highly specialized; inhabits permanent freshwater marshes with broad expanses of cattails, sawgrass, or other tall, emergent grasses, and with scattered clumps of bushes or small trees with a low and distant horizon for visibility.

SPECIAL HABITAT REQUIREMENTS: A permanent water source supporting adequate quantities of the apple snail.

NEST: Often nests in loose colonies, sometimes in or adjacent to colonies of herons, egrets, and anhingas. Males construct nests up to 8 feet above water in cattails, reeds, or bulrushes, or in willows or other shrubs or trees growing in water. Also nests in areas with tree islands dominated by dead trees and shrubs, or on artificial nest platforms.

FOOD: Feeds exclusively on the apple snail, which it sights while flying slowly low over water, or while perching on an old stake, a mound of aquatic debris, or a cattail clump.

REFERENCES: Brown and Amadon 1968, Heintzelman 1979, Mackenzie 1977, Sprunt 1955, Stieglitz and Thompson 1967, Terres 1980.

Mississippi Kite

Ictinia mississippiensis



L12"

RANGE: Breeds from central Arizona to north-central Kansas, southern Illinois, western Kentucky, the northern portions of the Gulf States and South Carolina south to central and southeastern New Mexico across the Gulf Coast and north-central Florida. Expanding range along its northern border. Winters in South America.

STATUS: Common in the southern Great Plains, uncommon in the Southeast.

HABITAT: Inhabits forests, open woodlands, and prairies. Found on the prairies of Kansas and in baldcypress swamps and pinelands in the Gulf States, scrub oak country in Oklahoma, and mesquite-sand sagebrush rangeland in Texas.

NEST: In the East, nests in riparian habitats, or in large pines, oaks, and sweetgums of large woods. In the Great Plains, nests in shelterbelts, farm woodlots, lawn trees in towns, or any small grove of trees. Also nests in scrub oaks and mesquite. Depending on the tree, places nest from 10 to 135 feet above ground. In Arizona, nests in cottonwoods taller than 50 feet in open groves or in scattered clumps surrounded by dense riparian scrubland of saltcedar and velvet mesquite 6.5 to 33 feet tall.

FOOD: Primarily consumes insects caught in the air, including grasshoppers, locusts, cicadas, katydids, large beetles, and dragonflies; also eats small snakes, lizards, and frogs.

REFERENCES: Brown and Amadon 1968, Glinski and Ohmart 1983, Heintzelman 1979, Kaufman in Farrand 1983a, Oberholser 1974a, Parker and Ogden 1979, Sprunt 1955, Terres 1980.

Bald Eagle

Haliaeetus leucocephalus



RANGE: Breeds from central Alaska and northern Yukon across Canada to Labrador and Newfoundland, south locally to the Aleutian Islands, southern Alaska, central Arizona, southwestern and central New Mexico, Baja California, and the Gulf Coast; very locally distributed in the interior of North America. Winters generally throughout the breeding range, but most frequently from southern Alaska and southern Canada southward.

STATUS: Endangered and threatened in parts of the lower 48 states.

HABITAT: Closely associated with lakes and large rivers in open areas, forests and mountains, and along seacoasts. In Alaska and Canada, where human disturbance is slight, habitat is composed of a narrow strip of land along lakeshores and rivers that provides trees for nesting, fishing, and loafing. Needs large trees adjacent to water, preferably snags, but also live trees or boulders that provide good visibility, for perching. Winters in coastal habitats and inland where ice-free waters allow access to fish.

SPECIAL HABITAT REQUIREMENTS: Large bodies of water containing abundant fish resources, large trees for nesting, perching, and roosting, and freedom from human disturbance.

NEST: Prefers to build a large, heavy nest 10 to 150 feet above ground in very tall living trees, usually close to water. If suitable trees are not available, nests are built on rocky cliffs or on the ground. Shows strong attachment to the nest site, and characteristically adds new material to the nest each year.

FOOD: Feeds primarily on fish it catches or takes from an osprey. Will feed on waterfowl and other birds, carrion, small- to medium-sized mammals, and turtles. Inland, subsists mainly on dead waterfowl during winter.

REFERENCES: DeGraff et al. 1980, Evans 1982, Fielder 1982, Grubb and Kennedy 1982, Heintzelman 1979, Mackenzie 1977, Sprunt 1955.

Northern Harrier

Circus cyaneus
(formerly Marsh Hawk)



RANGE: Breeds from northern Alaska to southern Quebec and Newfoundland south to Baja California, southern Arizona, southern and eastern Texas, southern Illinois, and southeastern Virginia. Winters from Alaska (casually) and southern British Columbia east to South Dakota, southern Ontario, and Massachusetts south through the United States to South America.

STATUS: Common; populations are increasing slightly in the Southwest, and declining in the Northeast and Midwest.

HABITAT: Typically inhabits sloughs, wet meadows, fresh or salt marshes, swamps, prairies and plains. Generally roosts on the ground or perches on very low objects such as fence posts or tree stumps. During the non-breeding season, inhabits areas far removed from nesting habitat. Roosts in undisturbed fields or marshes in winter.

SPECIAL HABITAT REQUIREMENTS: Open country with herbaceous or low woody vegetation for concealing nests.

NEST: Nests singly or sometimes semi-colonially, on the ground in a variety of sites, but usually near or above water. Nests in tall grass in open fields, in swamps with low shrubs and clearings, sometimes built up over water on a stick foundation, sedge tussock, or willow clump, or on a knoll of dry ground.

FOOD: Hunts for food, primarily on the wing, over fields, marshes, and meadows, taking a wide variety of prey including mammals, birds, amphibians, reptiles, insects, and fishes. Mostly eats small mammals.

REFERENCES: DeGraff et al. 1980, Evans 1982, Heintzelman 1979, Low and Mansell 1983, McAtee 1935, Sprunt 1955, Tate and Tate 1982, Terres 1980.

Sharp-shinned Hawk

Accipiter striatus



RANGE: Breeds from western and central Alaska and northern Yukon to southern Labrador and Newfoundland, south to central California, southern Texas, the northern parts of the Gulf States, and South Carolina. Winters from southern Alaska, the southernmost portions of the Canadian Provinces south through the United States to Panama.

STATUS: Fairly common; the population appears to be recovering from earlier declines that occurred until the early 1970's in the eastern United States.

HABITAT: Primarily inhabits coniferous and mixed conifer-birch-aspen forests of the Canadian and Transition life zones northward to the Arctic tree line. Less commonly inhabits other woodland types except in mountainous areas. During migration and in winter it may occur in almost any type of habitat containing trees or shrubs.

SPECIAL HABITAT REQUIREMENTS: Dense coniferous-deciduous forest.

NEST: Usually nests in trees with dense foliage, primarily conifers, from 6 to 90 feet, typically 30 to 35 feet above ground and below a well-developed canopy. Nests may be in small groves of conifers surrounded by deciduous trees. Generally constructs a new nest each year in the immediate area of the previous year's nest.

FOOD: Feeds primarily on birds sighted while flying over forest floor, meadows, and brushy pastures. Sparrow-sized birds are taken most often, but occasionally attacks birds larger than itself. Also eats a few small mammals, reptiles, and insects.

REFERENCES: DeGraff et al. 1980, Evans 1982, Heintzelman 1979, Jones 1979, Platt 1976, Reynolds et al. 1982, Tate and Tate 1982.

Cooper's Hawk

Accipiter cooperii



RANGE: Breeds from southern British Columbia and central Alberta to southern Quebec and Maine south to Baja California, Mexico, Louisiana, central Mississippi, Alabama, and Florida. Winters from Washington, Colorado, and southern Minnesota to New England south through the southern United States, to Costa Rica.

STATUS: Uncommon.

HABITAT: Inhabits various types of mixed and deciduous forests and open woodlands including small woodlots, riparian woodlands in dry country, open arid pinyon woodlands, and forested mountainous regions. May use almost any type of habitat containing trees or shrubs during winter and in migration.

SPECIAL HABITAT REQUIREMENTS: Mature coniferous or deciduous woodlands.

NEST: Usually nests in deciduous or coniferous trees near the edge of a wooded area, with large open fields and water nearby. Places nest from 20 to 60 feet above ground (usually 35 to 45 feet). Occasionally uses old crow nests.

FOOD: Hunts from inconspicuous perches, and catches its prey, primarily birds, by surprise. Consumes medium-sized birds such as thrushes, jays, starlings, and quail primarily but also takes smaller birds and larger birds up to the size of ruffed grouse. Also eats chipmunks, red squirrels, rabbits, other small mammals, amphibians, and insects.

REFERENCES: DeGraff et al. 1980, Evans 1982, Heintzelman 1979, Jones 1979, Reynolds et al. 1982.

Northern Goshawk

Accipiter gentilis
(formerly Goshawk)



RANGE: Breeds from western and central Alaska and northern Yukon to Labrador and Newfoundland, south to southern Alaska, central California, southern New Mexico, western South Dakota, northern Minnesota, and northwestern Connecticut, and in the northern Appalachian Mountains. Winters throughout the breeding range may extend as far south as the Gulf States during periodic invasions related to food shortage.

STATUS: Uncommon to rare but increasing; range is expanding southward in Appalachians.

HABITAT: Inhabits mixed hardwood and coniferous forests in temperate and boreal regions, from sea level to tree line. Prefers woodlands with intermediate canopy coverage interspersed with fields or wetlands, especially in remote areas.

SPECIAL HABITAT REQUIREMENTS: Extensive mixed woodlands with large trees for nesting.

NEST: Prefers to nest in large hardwood trees 30 to 40 feet above ground, where clear, level access is afforded by a stream or other opening. Frequently selects birch, maple, aspen, and beech for nesting trees; occasionally selects juniper, pine, spruce, and fir. Usually builds a new nest each year, but may build on top of an old hawk nest.

FOOD: Hunts for prey in dense woodlands, clearings, and open fields. In one study, its diet consisted of 54 percent birds, 37 percent mammals, and 9 percent insects. Eats grouse, quail, pheasants, small hawks, owls, crows, gulls, ducks, doves, thrushes, rabbits, squirrels, chipmunks, mice, woodchucks, muskrats, weasels, shrews, grasshoppers, and caterpillars.

REFERENCES: Cramp and Simmons 1980, DeGraff et al. 1980, Evans in Farrand 1983a, Heintzelman 1979, Jones 1979, McAtee 1935, Shuster 1980, Terres 1980.

Common Black-Hawk

Buteogallus anthracinus
(formerly Black Hawk)



L 20" W 48"

RANGE: Resident in central Arizona, southwestern Utah, southern New Mexico, and western Texas, south through Central America to Colombia (northernmost populations move southward during winter).

STATUS: Rare; threatened in Arizona and New Mexico.

HABITAT: An obligate of riparian areas. Optimum habitat consists of a flowing stream bordered by mature riparian forests. Also inhabits broad alluvial valleys, narrow rocky canyons, or marshes near the coast.

SPECIAL HABITAT REQUIREMENTS: Mature, relatively undisturbed habitat with a permanent water source and tall (75 to 100 feet) trees for nesting.

NEST: Nests in trees from 15 to 100 feet above ground, preferably within a grove of trees rather than in a lone tree. Builds nests in cottonwood, sycamore, alder, mesquite, willow, velvet ash, ponderosa pine and Douglas-fir. May use same nest for successive years.

FOOD: Prefers to fish in streams of low to moderate gradient, less than one foot deep with scattered boulders and some low or fallen branches. Usually locates prey while flying but also hunts from a perch. Eats a varied assortment of prey, including beach and land crabs, frogs, fishes, crayfish, reptiles, small mammals, birds, and insects.

REFERENCES: Heintzelman 1979, Oberholser 1974a, Schnell 1979.

Harris' Hawk

Parabuteo unicinctus



L 18" W 43"

RANGE: Resident in southern Kansas, and from southeastern California (recently reintroduced), southern Arizona, southern New Mexico, and central Texas south to South America.

STATUS: Fairly common.

HABITAT: Inhabits arid desert scrub of mesquite, palo verde and large cacti in the Southwest, river woodlands, and brushy flatlands. Infrequently found in yucca, cactus, creosotebush deserts, and oak-juniper habitats. Commonly perches on tops of telephone poles, trees, and bushes; on large cacti; and in snags.

SPECIAL HABITAT REQUIREMENTS: Thorn-scrub habitats.

NEST: Nests from 5 to 30 feet up in cactus, mesquite, hackberry, yucca, Spanish-bayonet, paloverde, ironwood, cottonwood, ebony, and other trees. May nest in pairs or in trios with an extra male that also brings prey to the nest.

FOOD: Consumes a diet comprising 57 percent mammals, 35 percent birds, and 7 percent lizards. Feeds on rabbits, wood rats, mice, night-herons, teal, flickers, and other birds and mammals.

REFERENCES: Harrison 1979, Heintzelman 1979, Oberholser 1974a, Sprunt 1955, Terres 1980, Terrill in Farrand 1983a.

Gray Hawk

Buteo nitidus



L 15" W 35"

RANGE: Breeds in southern Arizona and southern Texas (the northwestern extreme of its breeding range) south to South America. Northernmost populations usually migrate south in nonbreeding season.

STATUS: Rare.

HABITAT: Is found primarily in riparian willow, cottonwood, and sycamore groves in the San Pedro and Santa Cruz river drainages of Arizona. Inhabits mature woodlands of river valleys and nearby semiarid mesquite and scrub grasslands.

SPECIAL HABITAT REQUIREMENTS: Stands of cottonwood and willow near rivers for nesting.

NEST: The small nest is placed from 20 to 40 feet up in cottonwood, hackberry, or mesquite along streams or rivers.

FOOD: Prefers to feed on lizards and small snakes, and frequently eats beetles and large grasshoppers. Also catches and eats rabbits, squirrels, mice, quail, young doves, and fishes.

REFERENCES: Heintzelman 1979, Oberholser 1974a, Terres 1980, Terrill in Farrand 1983a.

Red-shouldered Hawk

Buteo lineatus



L 16" W 40"

RANGE: Breeds from northern California south, west of the Sierra Nevada divide, to Baja California; and from eastern Nebraska, central Minnesota, southern Ontario, and southern New Brunswick south to Mexico. Winters primarily from eastern Kansas and central Missouri to southern New England southward, but also sporadically throughout breeding range.

STATUS: Common, but population is unstable.

HABITAT: Inhabits moist, well-drained woodlands, wooded river swamps, bottomlands, and wooded margins of marshes, often close to cultivated fields. Seems to prefer mature forests and is usually more common in lowland areas than in mountainous regions.

SPECIAL HABITAT REQUIREMENTS: Riparian deciduous woodlands with tall trees for nesting.

NEST: Nests 20 to 60 feet above ground in tall trees. Usually builds nest 35-45 feet above ground on a main fork and close to the tree trunk. Has built nests in oak, pine, baldcypress, mangrove, cottonwood, birch, beech, sycamore, yellow-poplar, ash, sweetgum and maple. Occasionally uses an abandoned hawk, crow, or squirrel nest as a foundation for a new nest; often uses the same nest site year after year.

FOOD: Perches on a fence post, tree, or telephone pole and overlooks a meadow, marsh, open field, or forest to sight prey. Feeds primarily on small mammals but also takes rabbits, squirrels, small birds, frogs, small snakes, toads, lizards, fishes, and large insects.

REFERENCES: Bednarz and Dinsmore 1982, DeGraff et al. 1980, Forbush and May 1955, Heintzelman 1979, McAtee 1935, Portnoy and Dodge 1979, Sprunt 1955, Stewart 1949, Tate and Tate 1982.

Broad-winged Hawk

Buteo platypterus



L 13" W 33"

RANGE: Breeds in central Alberta and central Saskatchewan, and from central Manitoba to New Brunswick and Nova Scotia south to eastern Texas, the Gulf Coast and Florida. Winters in southern Florida and from Mexico to South America.

STATUS: Common throughout range.

HABITAT: Inhabits continuous dry woodlands of oaks, beeches, maples, and mixed coniferous-hardwoods around lakes, streams, and swamps. In migration when conditions are favorable, forms large flocks, or "kettles," soars to the top of thermals, and then glides to another, thus saving energy during the long flight to its wintering area.

NEST: Normally nests near water in a variety of tree species, from 25 to 90 feet, but as low as 3 to 10 feet, above ground. Nest site preference is probably related to life form of the tree species and characteristics of the site rather than to prevalence of a particular tree species. Black and yellow birch are commonly selected for nesting in New England. Sometimes uses old crow, hawk, or squirrel nests.

FOOD: Hunts from perch in deep, shady woodlands or while flying over treetops or open meadows. Feeds largely on small mammals such as mice, moles, and shrews, occasionally red squirrels and chipmunks; also eats snakes, frogs, lizards, large larvae of night-flying moths, caterpillars, grasshoppers, beetles, crickets, fiddler crabs, crayfish, sometimes small fish, and some small birds.

REFERENCES: DeGraff et al. 1980, Evans in Farrand 1983a, Forbush and May 1955, Heintzelman 1979, Matray 1974, Sprunt 1955, Terres 1980.

Short-tailed Hawk

Buteo brachyurus



RANGE: Resident locally in peninsular Florida, from St. Marks and San Mateo south to Lake Okeechobee. Winters mostly south of Lake Okeechobee and in Central and South America.

STATUS: Rare.

HABITAT: A tropical species that barely reaches the United States in Florida, this buteo is found primarily in mixed woodland-savannah habitats, but also in mangrove and baldcypress swamps adjacent to forests, and along streams and the borders of lakes. Often perches in tall trees.

NEST: Nests in the topmost branches of tupelos, pines, magnolias, or baldcypresses, from 40 to 100 feet above ground or in the top of mangroves.

FOOD: Feeds on a great variety of birds, but primarily meadowlarks and red-winged blackbirds. Also feeds on some small mammals, reptiles, and amphibians.

REFERENCES: Heintzelman 1979, Ogden 1974, Ogden in Farrand 1983a, Sprunt 1955, Terres 1980.

Swainson's Hawk

Buteo swainsoni



L 18" W 49"

dark
phase

light
phase

RANGE: Breeds locally in east-central Alaska, Yukon, and Mackenzie, and from central Alberta and central Saskatchewan to western Illinois south to southern California, central and southern Texas, and western Missouri. Winters primarily on the pampas of southern South America, casually north to the southwestern United States and southeastern Florida.

STATUS: Common; population has decreased in the southern Great Plains.

HABITAT: Inhabits prairies, plains, deserts, large mountain valleys, savannahs, open pine-oak woodlands, and cultivated lands with scattered trees.

NEST: Nests in isolated trees, in shrubs and trees along wetlands and drainages, in windbreaks in fields and around farmsteads, in giant cactus, or on the crossbars of telephone poles. Occasionally nests on the ground, on low cliffs, on rocky pinnacles, or on cutbanks. May build nest up to 100 feet above ground in cottonwoods, or lower in willows or other shrubs. May repair and use same nest year after year; sometimes builds on old black-billed magpie nests.

FOOD: Hunts primarily from perches such as fence posts or low trees and from a vantage point on the ground. Diet consists of small mammals, birds, fishes, salamanders, frogs, snakes, and insects.

REFERENCES: Dunkle 1977, Evans in Farrand 1983a, Heintzelman 1979, Sprunt 1955, Tate and Tate 1982, Terres 1980.

White-tailed Hawk

Buteo albicaudatus



L 21" W 48"

RANGE: Resident from central and southeastern Texas south to South America.

STATUS: Uncommon.

HABITAT: Inhabits saltgrass flats of coastal grasslands, and open grassy ranges and chaparral country with scattered mesquite, yucca, and large cacti farther inland. Perches on bushes, trees, utility wires, or on the ground.

NEST: Nests on prairies, in brush, or in fringes of timber in sizeable bushes or small trees, 5 to 15 feet above ground. Prefers to nest on a ridge with a view all around. Nest plants include large cactus, yucca, and scrub oaks. May use the same nest in successive years.

FOOD: Feeds extensively upon rabbits; also eats cotton rats, lizards, snakes, frogs, grasshoppers, beetles, cicadas, and other insects.

REFERENCES: Heintzelman 1979, Oberholser 1974a, Terres 1980.

Zone-tailed Hawk

Buteo albonotatus



L 19" W 47"

RANGE: Breeds from central Arizona, southern New Mexico, and western Texas south to South America. Very rare north of Mexico in winter.

STATUS: Locally fairly common.

HABITAT: Inhabits deep, rough, and rocky wooded canyons and tree-lined rivers along middle slopes of desert mountains, especially in open deciduous or pine-oak woodland.

SPECIAL HABITAT REQUIREMENTS: Large trees for nesting.

NEST: Builds a bulky nest in large trees, usually cottonwoods along streams and rivers, 25 to 100 feet above ground in leafy top. Rarely nests in mesquites.

FOOD: Eats chipmunks, quail and small birds, lizards, small fishes, and frogs (little is known about diet).

REFERENCES: Heintzelman 1979, Oberholser 1974a, Terres 1980.

Red-tailed Hawk

Buteo jamaicensis



RANGE: Breeds from western and central Alaska and central Yukon to New Brunswick and Nova Scotia south to Central America. Winters from southern Canada throughout the remainder of the breeding range.

STATUS: Common, but population is declining.

HABITAT: Inhabits a wide variety of different habitats throughout its range, preferring mixed country of open pasture, fields, meadows, or swampy areas interspersed with coniferous or deciduous woods. Inhabits deserts and plains with scattered trees and open mountain forests, generally avoiding dense, unbroken woodlands and tundra.

NEST: Usually nests in a tall tree in or at the edge of a woodland, or in an isolated tree in an open area. Frequently selects the largest and tallest tree (of a wide variety of species) available. Constructs nest next to the trunk in a crotch from 35 to 90 feet above ground. In treeless areas, nests on rocky cliffs, shrubs, or cactus.

FOOD: Frequently hunts for prey while perching in snags, live trees, or on poles in rather open areas or at forest edges. Also locates prey while soaring. Primarily eats small mammals; also eats birds, reptiles, and some insects.

REFERENCES: Austin 1964, Bednarz and Dinsmore 1982, DeGraff et al. 1980, Evans in Farrand 1983a, Fitch et al. 1946, Forbush and May 1955, Heintzelman 1979, Terres 1980.

Ferruginous Hawk

Buteo regalis



RANGE: Breeds from eastern Washington, southern Alberta, and southern Saskatchewan south to eastern Oregon, Nevada, northern and southeastern Arizona, northern New Mexico, north-central Texas, western Oklahoma, and Kansas. Winters primarily from the central and southern parts of breeding range south to Mexico.

STATUS: Common; population is stable or declining slowly.

HABITAT: Inhabits the semiarid western plains and arid intermountain regions; prefers relatively unbroken terrain, with scattered trees, rock outcrops, or tall trees along creek bottoms available for nesting sites. Generally winters on the southern plains.

SPECIAL HABITAT REQUIREMENTS: Open country with elevated nesting sites.

NEST: Prefers tall trees for nesting; will use a wide variety of sites, including ground nests on riverbed mounds, cutbanks, low hills, buttes and small cliffs, in short trees in open country, powerline structures, and haystacks. Tree nests are usually in the upper canopy, from 6 to 55 feet above ground. Nests are often used year after year.

FOOD: Hunts from a perch, while soaring, during low, rapid flight over open country, or while systematically searching and hovering at 40 to 60 feet. One study found its diet to be 70 percent mammals, 27 percent birds, and 3 percent reptiles. Feeds primarily on rabbits, ground squirrels, and prairie dogs; also takes mice, rats, gophers, birds, snakes, locusts, and crickets.

REFERENCES: Blair and Schitoskey 1982, Evans 1982, Heintzelman 1979, Snow 1974a, Sprunt 1955, Tate and Tate 1982, Weston 1969, Woffinden and Murphy 1983.

Rough-legged Hawk

Buteo lagopus



RANGE: Breeds from western and northern Alaska, northern Yukon, and northern Labrador south to northern and southeastern Mackenzie, east to northern Quebec and Newfoundland; also from Kodiak Island and Umnak in the eastern Aleutian Islands and the Arctic Islands north to Prince Patrick, Victoria, Bylot, and southwestern Baffin Islands. Winters from south-central Alaska (casually) and southern Canada south to southern California, southern Arizona east to southern Texas, Missouri, Tennessee, and Virginia, casually to eastern Texas and the Gulf Coast. Concentrates in areas of high prey density during winter.

STATUS: Most common hawk of the American arctic.

HABITAT: Inhabits open tundra and mountainsides; does not inhabit forests unless there is much open ground. Essentially an open country dweller that occupies a large range in its seasonal wanderings. In winter, prefers conifer groves for roosting and open, treeless areas for hunting.

NEST: Nests primarily on cliffs along river bluffs, but is flexible in selecting nesting substrate. Locates nests usually under overhangs on rocky cliffs, outcroppings, and ledges; occasionally nests in stunted trees or on the ground. Often returns to the same nest for many years.

FOOD: Hunts for food in wet meadows, bogs, and riparian areas. Generally seeks prey from the air rather than from a perch. Microtine rodents such as brown lemming, collared lemming, tundra vole, Alaska vole, red-backed vole, and other small mammals comprise the bulk of the diet. Shifts to other prey when rodents become scarce. Also consumes young ptarmigan, arctic ground squirrels, and sometimes small rabbits. During the breeding season, may consume up to 20 percent of diet as birds; during winter, consumes mammalian prey almost exclusively.

REFERENCES: Heintzelman 1979, Sprunt, 1955, Terres 1980, White and Cade 1971, Zarn 1975.

Golden Eagle

Aquila chrysaetos

im.



L 32" W 78"

RANGE: Breeds from northern and western Alaska east to Labrador, south to southern Alaska, Baja California, western and central Texas, western Oklahoma, and western Kansas; in eastern North America to New York and New England. Winters from south-central Alaska and the southern portions of the Canadian provinces south throughout the breeding range, rarely to coastal South Carolina.

STATUS: Fairly common in the West, rare in the East.

HABITAT: Inhabits open country, from barren areas to open coniferous forests, primarily in hilly and mountainous regions, but also in rugged deserts, on the plains, and in tundra. Prefers large trees with large horizontal branches and cliffs for roosting and perching. In the West, often moves down from the mountains onto the plains and valleys for winter.

SPECIAL HABITAT REQUIREMENTS: Elevated nest sites, especially cliffs, that are isolated from human disturbance and are close to hunting areas.

NEST: Usually nests on cliff ledges, preferably overlooking grasslands, but also nests in trees or on the ground. In the western mountains, nests at elevations of 4,000 to 10,000 feet above sea level. May use the same nest year after year, or pairs may use alternate nests in successive years.

FOOD: An opportunist; hunts for a variety of prey by soaring over open country or by sighting prey from perch. Feeds primarily on mammals (mainly lagomorphs), but also marmots, prairie dogs, ground squirrels, weasels, woodrats, skunks, and mice, rarely on larger mammals. Also eats grouse, pheasants, owls, hawks, rock doves, magpies, and other birds, as well as rattlesnakes and some carrion.

REFERENCES: DeGraff et al. 1980, Heintzelman 1979, Jollie 1943, McGahan 1968, Snow 1973, Terres 1980.

American Kestrel

Falco sparverius



RANGE: Breeds from western and central Alaska and southern Yukon to northern Ontario, southern Quebec, and southern Newfoundland south to Mexico. Winters from south-central Alaska, southern British Columbia, and northern United States south throughout the breeding range to Panama.

STATUS: Common.

HABITAT: Widely distributed in habitats that include deserts, forest openings, marshes, grasslands, agricultural and suburban areas, towns, and cities. Frequently perches on fence posts, utility poles and wires, and in trees. Occupies the same types of habitats during winter as during the breeding season.

SPECIAL HABITAT REQUIREMENTS: Open country with low vegetation, cavities in trees with dbh greater than 12 inches, and elevated perches from which to sight prey.

NEST: Prefers to nest in natural tree cavities with tight-fitting entrances, or in cavities excavated by flickers. If these are unavailable, nests in a variety of sites including niches in rocky cliffs, under eaves of buildings, in old magpie nests, in cavities in cacti, in unused chimneys, or in nest boxes. Nest sites are usually along roadways, streams, ponds, or forest edges, from 4 to 65 feet above ground, though typically from 10 to 35 feet.

FOOD: Hunts from a perch or while hovering over areas with short, open vegetation. Primarily eats insects such as grasshoppers, crickets, and beetles in summer, but also takes mice and other small mammals, birds, lizards, toads, frogs, and small snakes; rarely takes spiders or worms.

REFERENCES: Balgooyen 1976, DeGraff et al. 1980, Evans in Farrand 1983a, Heintzelman 1979, McAtee 1935, Smith et al. 1972, Thomas et al. 1979.

Merlin

Falco columbarius



RANGE: Breeds from northwestern Alaska and northern Yukon to Labrador and Newfoundland, south to southern Alaska, eastern Oregon, northern Minnesota, southern Quebec, New Brunswick, and Nova Scotia. Winters west of the Rockies from south-central Alaska, southern British Columbia, Wyoming, and Colorado southward, locally across southern Canada, and in the eastern United States from Maryland, the Gulf Coast, and southern Texas to South America.

STATUS: Uncommon.

HABITAT: Inhabits open areas such as forest edges, bogs, and lakes in boreal and moist Pacific Coastal forests, and prairie-parkland of the northern Great Plains. Some remain in prairie habitat even in winter; others will use almost any habitat type encountered in its winter range.

NEST: Generally nests in trees from 5 to 60 feet above ground, often in old stick nests of crows, ravens, magpies, or other raptors, in or near open areas, and generally near water. Occasionally nests on the ground, on bare ledge of a cliff, or in cavities in trees. Prairie birds prefer to nest in isolated groves of trees near water, and in wooded areas along rivers, generally in coniferous trees.

FOOD: Sights prey from an inconspicuous perch or during flight. Preys almost entirely on small to medium-sized birds; also takes large insects, scorpions, spiders, crayfish, toads, small snakes, bats, and small mammals.

REFERENCES: Evans 1982, Fox 1964, Heintzelman 1979, McAtee 1935, Sprunt 1955, Trimble 1975.

Peregrine Falcon

Falco peregrinus



RANGE: Breeds from northern Alaska, Banks, Victoria, southern Melville, Somerset and northern Baffin Islands, and Labrador south to Baja California, southern Arizona, New Mexico, western and central Texas, and Colorado; recently re-introduced and re-established as a breeding bird in parts of the northeastern United States. Winters from southern Alaska, the Queen Charlotte Islands, coastal British Columbia, the central and southern United States, and New Brunswick south to South America.

STATUS: Rare and endangered; catastrophic decline primarily due to organochlorine pesticides.

HABITAT: Usually inhabits open country from tundra and seacoasts, to high mountains and more open forested regions, preferably where there are rocky cliffs with ledges overlooking rivers, lakes, or other water and an abundance of birds. Sometimes breeds in cities.

SPECIAL HABITAT REQUIREMENTS: Cliffs or other nesting habitat near water, and an abundance of prey.

NEST: Prefers to nest in a shallow depression scraped in gravel and debris on a high cliff ledge, pothole, or small cave that provides sanctuary from disturbance. Bluffs, slopes, pinnacles, cutbanks, and seastacks are also used as nest sites in the far north. Other nest sites include old stick nests of ravens and hawks, ledges of tall buildings, and historically, holes and stubs of large trees. Tends to return to the same nesting cliff.

FOOD: Pursues prey, primarily birds, after sighting from perch or while soaring. Small- to medium-sized birds are usually captured in flight; birds too large to be carried are knocked to the ground. Feeds on a wide variety of birds; occasionally takes mammals, some insects, and fishes.

REFERENCES: Cade 1960, DeGraff et al. 1980, Evans 1982, Heintzelman 1979, Hickey 1942, Hickey and Anderson 1969, Terres 1980, White and Cade 1971.

Prairie Falcon

Falco mexicanus



RANGE: Breeds from southeastern British Columbia, southern Alberta, southern Saskatchewan, and northern North Dakota south to Baja California, New Mexico, and northern Texas. Winters from the breeding range in southern Canada south to Mexico.

STATUS: Locally common.

HABITAT: Inhabits prairies, deserts, riverine escarpments, canyons, foothills, and mountains in relatively arid western regions. Occupies open, treeless terrain that accommodates its low-level style of hunting. Wintering birds are found away from the breeding areas in intermontane valleys and on the Great Plains.

SPECIAL HABITAT REQUIREMENTS: Suitable nesting sites on cliffs in open country free of human disturbance.

NEST: Nests on cliffs, from low rock outcrops of 30 feet to vertical cliffs 400 feet high. Prefers cliffs with a sheltered ledge with loose debris or gravel for a nest scrape, overlooking treeless country for hunting. Also nests in larger caves in cliffs and vertical or columnar cracks with lodged material. Sometimes uses old nests of ravens, hawks, or eagles.

FOOD: Typically hunts from perches or in low, rapid, searching flight, usually capturing prey on or near the ground. Feeds on a variety of prey including ducks, prairie chickens, quail, pigeons, doves, sparrows and other small birds, prairie dogs, mice, ground squirrels, young rabbits, grasshoppers, and lizards.

REFERENCES: Enderson 1964, Evans 1982, Heintzelman 1979, McAtee 1935, Snow 1974b, Sprunt 1955, Terres 1980.

Plain Chachalaca

Ortalis vetula
(formerly Chachalaca)



L 18" W 26"

RANGE: Resident from the lower Rio Grande Valley to Costa Rica. Introduced on Sapelo, Blackbeard, and Little St. Simons Islands, Georgia.

STATUS: Locally common to uncommon; largely restricted to parks and refuges because of clearing of habitat for residential and agricultural purposes.

HABITAT: Prefers wooded stream beds with thick growths of ebony blackbead, hackberry, mesquite, and thick, shrubby undergrowth. Rarely found far from water; also inhabits thick growths of sugarberry, Texas ligumvitae, huisache, cedar elm, and willow. Has adapted well to living in relatively small (1 to 5 acres) tracts of dense woodland vegetation.

SPECIAL HABITAT REQUIREMENTS: Dense brushland.

NEST: Constructs a small, flimsy nest or uses old nests of birds such as the yellow-billed cuckoo, groove-billed ani, or curve-billed thrasher. Nests in trees, or in vines supported by trees, from 3 to 33 feet above ground. Most commonly uses cedar elm, huisache, sugarberry, anacua, and ebony blackbead. Spanish moss and tangled vines commonly support and conceal the nest.

FOOD: Eats berries, especially hackberries, along with the fruit of mesquite, mangoes, junipers, palmettos, persimmons, wild grapes, and figs; also eats green leaves, buds and shoots of plants, grain (especially cracked corn), and some insects.

REFERENCES: Johnsgard 1975a, Marion 1974, Marion and Fleetwood 1978, Oberholser 1974a, Terres 1980.

Gray Partridge

Perdix perdix



L 10"

RANGE: Widely introduced in North America and established locally from southern British Columbia to southwestern Quebec, New Brunswick, and Nova Scotia south to northern Nevada, northern South Dakota, central Indiana, and northern Vermont. Native to Eurasia.

STATUS: Locally abundant.

HABITAT: Has adapted well to diverse and intensive agricultural land use practices. Prefers cropland areas interspersed with native grassland, but also inhabits brushy canyons and brushy stream bottoms in the West, irrigated agricultural lands, and gently rolling hay fields, grain fields, and pastures. In winter, needs protective woody cover during adverse weather and accessible food resources, such as waste grain and green plant material.

SPECIAL HABITAT REQUIREMENTS: Herbaceous cover for nesting, and grit (primarily obtained from gravel roads) for grinding food.

NEST: Nests in a shallow scrape in the ground, usually located in grasses, or near the edge of hay fields or grain fields, sometimes in alfalfa fields, or along fencerows or roadsides.

FOOD: Feeds on cultivated grains, seeds of grasses and herbs, and on insects. Obtains some of its water from succulent vegetation.

REFERENCES: Johnsgard 1975a, Kobriger 1983, McCabe and Hawkins 1946, Terres 1980, Weigand 1980.

Chukar

Alectoris chukar



L 10"

RANGE: Introduced widely in North America, and established locally from south-central British Columbia to central and eastern Montana south to Baja California, southern Nevada, northwestern New Mexico, and south-central Colorado. Native to Eurasia.

STATUS: Locally common.

HABITAT: Inhabits open, rocky, sagebrush-grassland habitats from below sea level to as high as 12,000 feet, on dry mountain slopes and canyons. Also inhabits areas with Mormon tea, bitterbrush, currant, and rabbitbrush; in the southern portion of its range it may be found in saltbush-grassland habitat, but generally avoids pinyon-juniper climax habitat. During hot weather, tends to concentrate near water provided by springs, seeps, and small perennial and intermittent streams, dispersing when surrounding vegetation greens up after rains. Moves to lower elevations in heavy snows. Roosts on the ground beneath sagebrush, under junipers, in the shelter of rock outcrops, and in open rocky places, but not in dense cover.

SPECIAL HABITAT REQUIREMENTS: Water source during hot weather in summer and early fall.

NEST: Nests in a depression scratched in the ground, constructed under shrubs or well concealed by rocks and brush in rocky areas. May occasionally have a dump nest.

FOOD: During summer and fall, feeds primarily on seeds of cheatgrass, Russian thistle, rough fiddleneck, and redstem filaree; also takes seeds of Indian ricegrass, curly dock, and mustard. Will also eat grass blades, stems and buds of a variety of plants, wild onion seeds, grasshoppers, and caterpillars.

REFERENCES: Christensen 1970, Johnsgard 1975a, Molini 1976.

Ring-necked Pheasant

Phasianus colchicus



RANGE: Introduced and established widely in North America, from southern British Columbia and central Alberta to northern Minnesota, southwestern Quebec, New Brunswick, and Nova Scotia south, at least locally, to southern interior California, Utah, northern and southeastern Texas, southern Illinois, Pennsylvania, New Jersey, and North Carolina. Native to Asia.

STATUS: Common.

HABITAT: Inhabits cultivated farmland interspersed with patches of brush or woodlots, especially areas with field border cover. Also inhabits fallow fields, brushy pastures, roadside hedgerows, cutover land, marshes, and meadows. Roosts mostly on the ground in weedy ditches, marshes, cattail swales, weed-grown fence rows, brush heaps, briar patches, and small farm-woodlots. In winter, needs protective cover such as marshes, thickets, shelterbelts, and heavy brush in ravines, along fencerows, and railroad right-of-ways, and an adequate supply of food.

SPECIAL HABITAT REQUIREMENTS: Agricultural land interspersed with dense protective cover.

NEST: Nests on the ground in a scratched-out depression, preferably among plants that make maximum growth during spring, such as alfalfa or coolseason grasses. Locates nest in fields of alfalfa, sweet clover, winter wheat, or other grasses or grains; along roadsides, fencerows, and hedgerows; or in brushy pastures or wetlands.

FOOD: Feeds primarily on plant foods, especially waste grains, but also on seeds of weeds and grasses, acorns, buds and soft parts of herbaceous vegetation, fleshy fruits, insects, snakes, and mice.

REFERENCES: Baxter and Wolfe 1973, Dale 1956, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1975a, Ratti in Farrand 1983a, Terres 1980.

Spruce Grouse

Dendragapus canadensis



RANGE: Resident from northern Alaska to northern Quebec, Labrador, New Brunswick, and Nova Scotia south to south-coastal and southeastern Alaska, northern Oregon, southeastern Idaho, northwestern Wyoming, western Montana, and southeastern Alberta to northern Minnesota east to northern Vermont, northern New Hampshire, and eastern Maine (range is generally congruent with that of the northern coniferous forest).

STATUS: Uncommon in most of the southern portions of its range.

HABITAT: Inhabits short-needled coniferous forests, especially where living branches reach the ground and where there are numerous, scattered forest openings of a few hundred square feet. In the northeast, prefers wet lowland edges; farther west, prefers higher ground. Generally prefers a mixture of jack pine or lodgepole pine and spruce, and a sparse ground cover. Males establish breeding territories in dense pine stands. Shows little fear of humans and often called "fool hen."

SPECIAL HABITAT REQUIREMENTS: Large tracts of coniferous forest.

NEST: Nests on the ground in well-concealed sites, often under low branches of spruce, jack pine, or white pine; in brush; in deep moss; or adjacent to a tree trunk or stump.

FOOD: During winter, consumes diet of nearly 100 percent conifer needles. In other seasons, consumes a variety of foods, including leaves, flowers, berries, seeds, pine needles, and a few insects. Needs a source of fine, mineral-rich gravel.

REFERENCES: Johnsgard 1973, Pendergast and Boag 1970, Robinson 1969, 1980, Robinson in Farrand 1983a.

Blue Grouse

Dendragapus obscurus



RANGE: Resident from southeastern Alaska, southern Yukon, and extreme southwestern Mackenzie south along the Pacific Coast to northern California; in mountains to central California, northeastern Nevada, northern Arizona, Colorado, and northern New Mexico; rare in mountains of southern California. Closely associated with Douglas-fir and true firs.

STATUS: Common.

HABITAT: Occupies a fairly vertical range in the western mountains, breeding at lower elevations in open stands of conifers or aspens with a brush understory, in meadows or in stands of mixed brush and herbs interspersed with bare ground adjacent to aspens or conifers. Males display in relatively open stands of trees or shrubs on earth mounds, rocks, logs, cutbanks, and occasionally tree limbs. During autumn, moves up from the open breeding range to stands of conifers or to timberline.

SPECIAL HABITAT REQUIREMENTS: Medium to large forest openings; shrubs, grasses, and forbs for nesting.

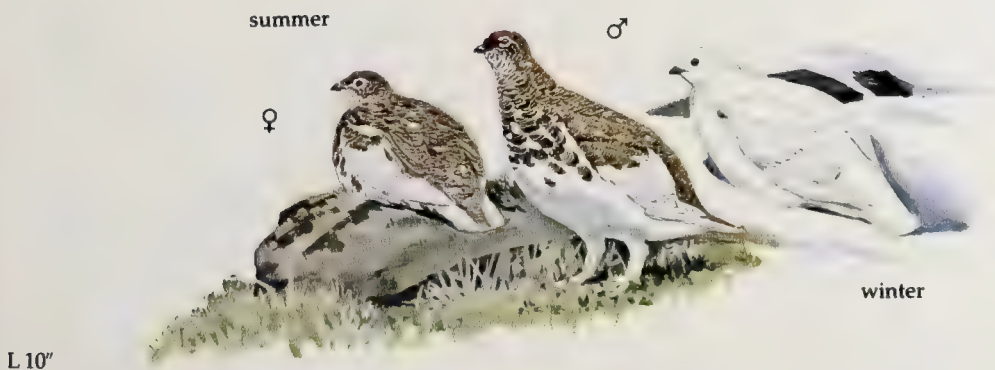
NEST: Nests in a shallow depression on the ground, well-concealed near logs or rocks, at the base of a tree, under sagebrush, or in the shelter of chokecherry, aspen, or cottonwood.

FOOD: During winter, eats diet limited to needles and buds of conifers, especially Douglas-fir, but also other firs, hemlock, and lodgepole pine. In other seasons, eats berries, flowers and leaves of herbaceous plants, and insects. In warm weather seldom far from a source of water. Can obtain necessary water from succulent vegetation or berries, if available.

REFERENCES: Beer 1943, Bendell and Elliott 1966, Harju in Farrand 1983a, Johnsgard 1973, Rogers 1968, Terres 1980, Verner and Boss 1980.

White-tailed Ptarmigan

Lagopus leucurus



RANGE: Resident from south-central Alaska, central Yukon, and southwestern Mackenzie south to southern Alaska, southern British Columbia, including Vancouver Island, and the Cascade Mountains of Washington, and along the Rocky Mountains from southwestern Alberta to northern New Mexico. Introduced into the high Sierra Nevada of California, Wallowa Mountains in Oregon, and the Uinta Mountains in Utah. Commonly migrates locally during winter to areas slightly below treeline.

STATUS: Locally common in alpine tundra.

HABITAT: Inhabits rocky tundra areas with sparse vegetation in high mountains. Breeds in territories adjacent to spruce-willow alpine timberline zone (krummholz) and also small windblown areas. Males tend to winter above tree line adjacent to breeding areas where wind prevents complete coverage of woody shrubs; females tend to winter in basins and drainages that are not as windblown and somewhat removed from tundra.

SPECIAL HABITAT REQUIREMENTS: Alpine tundra.

NEST: Nests on the ground in areas that become snowfree early in June and are somewhat protected from wind, such as under small shrubs or next to rocks larger than 6 inches. Females locate their nests near the fringe of a male's breeding territory, but more importantly, near brooding areas where vegetation is short and rocks 6 inches or larger cover more than 50 percent of the ground surface.

FOOD: During summer, primarily consumes seeds and leaves of smartweeds, sedges, clover, and willow; also takes various green leaves, flowers, and some insects. During winter in Colorado, consumes willow primarily, alder secondarily. In Alaska, consumes alder catkins primarily, willow and birch secondarily.

REFERENCES: Braun 1969; Braun in Farrand 1983a; Braun and Rogers 1971; Johnsgard 1973, 1983a; May and Braun 1972; Weeden 1967.

Ruffed Grouse

Bonasa umbellus



RANGE: Resident from central Alaska and northern Yukon to southern Labrador south to northwestern California, central and eastern Idaho, central Utah, Wyoming and Montana, central and southeastern Minnesota, Ohio, in the Appalachian Mountains to northern Georgia and northeastern Virginia; locally to western South Dakota; introduced and established in Iowa and Newfoundland.

STATUS: Fairly common; population fluctuates.

HABITAT: Inhabits successional to subclimax hardwood forests larger than 10 acres that have *Betula* or *Populus* present and an understory of small hardwoods, shrubs, and fruit-producing bushes (early successional stages of plant growth on logged-over areas are ideal). Male uses logs, rocks, or other elevated sites for drumming in spring. Frequents hedgerows and brushy patches in early fall; moves into more heavily wooded areas, especially coniferous cover in winter. Roosts in snow when snow is deep and soft, or may roost in trees or on the ground.

SPECIAL HABITAT REQUIREMENTS: Hardwood forests with some conifers, dense undergrowth, openings, and drumming sites for males.

NEST: Nests on dry ground in the shelter of a fallen log, rock, root, or low-hanging conifer limb, usually near the base of a tree. Commonly nests within 100 feet of a road, path, or clearing, and close to a source of water.

FOOD: During winter, feeds primarily on aspen buds, but also on buds of birch, alder, and hazel. In other seasons, consumes an extremely varied diet, including over 600 species of plants (seeds, fruits, leaves, and buds), insects, and other animals, although animal food is only predominate in the diet the first 2 weeks after hatching.

REFERENCES: Boag and Sumanik 1969, Bump et al. 1947, DeGraff et al. 1980, Johnsgard 1973, Rue 1973.

Sage Grouse

Centrocercus urophasianus



RANGE: Resident locally from central Washington, southern Idaho, Montana, southeastern Alberta, southwestern Saskatchewan and North Dakota, and western South Dakota south to eastern California, south-central Nevada, southern Utah, Colorado and northern New Mexico. Generally, associated with big sagebrush.

STATUS: Common (formerly widespread); range has been reduced, and its population is lower than it was 30 years ago.

HABITAT: Inhabits sagebrush-dominated rangelands, from the plains to the mountains, preferably where sagebrush provides 15 to 50 percent of the ground cover. Depends entirely upon forms of sagebrush, primarily big sagebrush, for food from October through May and for cover throughout the year. In spring, males prefer relatively open, rather than dense, sagebrush cover for strutting grounds. May move up to 50 miles or more throughout the year; occupies areas with exposed sagebrush during winter.

SPECIAL HABITAT REQUIREMENTS: Sagebrush-dominated rangelands.

NEST: Usually nests beneath sagebrush in a shallow depression on the ground. Usually locates nest in drier sites close to strutting grounds where shrub cover is less than 50 percent and vegetation is 10 to 20 inches tall. Moves young broods to moist areas, where there is a plentiful supply of insects and green plant material.

FOOD: In winter, feeds entirely on sagebrush leaves. Prefers Wyoming big sagebrush to mountain big sagebrush, thus maximizing proteins and minimizing monoterpenes. Also feeds (to a small extent) on alkali sagebrush and, in Idaho on black sagebrush. In other seasons, also feeds on forbs and some insects.

REFERENCES: Braun in Farrand 1983a, Dalke et al. 1963, Johnsgard 1973, 1983a, Patterson 1952, Remington 1983, Tate and Tate 1982.

Greater Prairie-Chicken

Tympanuchus cupido

(includes Attwater's Prairie-Chicken)



RANGE: Resident locally from eastern North Dakota, northwestern and central Minnesota, northern Wisconsin, and northern Michigan south to northeastern Colorado, Kansas, southern and northeastern Oklahoma, central Missouri, and southern Illinois; also in southeastern Texas.

STATUS: Endangered in Texas; uncommon and local; range and population reduced because of agriculture, burning, mowing, overgrazing, oil development, drainage, shooting, and urban development.

HABITAT: Inhabits stands of natural tall or midgrass prairie, especially where natural grasslands are interspersed with moderate amounts of small-grain cropland. Males favor slightly elevated open areas of short grassland for display grounds, which are approximately 1 acre in size and surrounded by dense grasses with some brush cover. Moderately tall vegetation is used for night roosting, and edges of tallgrass and midgrass for day resting. Requires a stable source of food rather than protective cover or shelter for winter.

SPECIAL HABITAT REQUIREMENTS: Shortgrass and tallgrass prairies.

NEST: Nests in a slight depression on the ground in a well-drained site that provides good concealment from above, within 1/2 mile of display grounds, in ungrazed meadows, natural prairie stands, or in clumps of prairie grasses, usually near an open area. Chooses brood habitat that is usually heavier than nesting habitat, in old fields, native grasses, or in cultivated pastures, where shade and a plentiful supply of insects and succulent plants are available.

FOOD: Consumes mostly insects from May to October, especially grasshoppers. Consumes primarily plant foods, including fruits, leaves, flowers, acorns, seeds of grasses and weeds, and grains the rest of the year.

REFERENCES: Johnsgard 1975a, 1983a, Jones 1963, Mackenzie 1977, Terres 1980.

Lesser Prairie-Chicken

Tympanuchus pallidicinctus



RANGE: Resident locally from southeastern Colorado, south-central Kansas, and western Oklahoma to extreme eastern New Mexico and the Texas Panhandle.

STATUS: Uncommon and local.

HABITAT: Inhabits arid natural grasslands of the southern Great Plains that are interspersed with shrubs 3 feet tall or less. In Colorado, occupies plant communities dominated by sand sagebrush, little bluestem, switchgrass, sideoats grama, and red threeawn. In Oklahoma and New Mexico, occupies a shinnery oak vegetation type. Needs small trees or shrubs such as shin oak, sagebrush, skunkbrush, sand plum, Havard oak, sand sagebrush, and fragrant sumac for shade during warm summer months. In spring and fall males congregate on display grounds which are relatively void of vegetation and have good visibility. Tall, perennial grasses are used for loafing in winter.

SPECIAL HABITAT REQUIREMENTS: Shin oak or sand sagebrush rangelands.

NEST: Nests on the ground in well-drained sites within 1/2 mile of display grounds. Builds nests that are well concealed from above in ungrazed meadows, natural prairie, or between grass clumps from previous years' growth, generally in tall, dense, perennial grasses.

FOOD: Primarily insectivorous during summer months. Consumes plant foods during the remainder of the year; leaf galls, catkins, leaves and acorns of shin oak can make up 70 percent of the seasonal diet; leaf and flower buds of fragrant sumac and the leaves of sand sagebrush are also important foods.

REFERENCES: Copelin 1963; Doerr and Guthery 1980; Hoffman 1963; Johnsgard 1975a, 1983a; Jones 1963; Taylor and Guthery 1980.

Sharp-tailed Grouse

Tympanuchus phasianellus



RANGE: Resident, at least locally, from central Alaska and central Yukon to northern Ontario and west-central Quebec, south to eastern Oregon, central Utah, central Colorado, central Nebraska, central Minnesota, central Wisconsin, northern Michigan, and southern Ontario.

STATUS: Locally common; population is down in the northern Great Plains.

HABITAT: Inhabits mid to tall grasslands interspersed with scattered woodlands, arid sagebrush, brushy hills, oak savannah, and edges of riparian woodland. Prefers habitats with several small openings, 1 to 10 acres in size, close together or a single large opening of 50 to 100 acres. In late summer and early autumn found mainly in open cover, grassy openings, or in low, scattered brush. Later, moves to thickets and open woods; in winter, to edges of brush, open woods, or swamps. Prefers tops of low to medium hills or ridges with short, sparse vegetation for courtship sites. Roosts in trees or shrubs in brushy cover.

SPECIAL HABITAT REQUIREMENTS: Grasslands interspersed with shrubs or trees and grainfields.

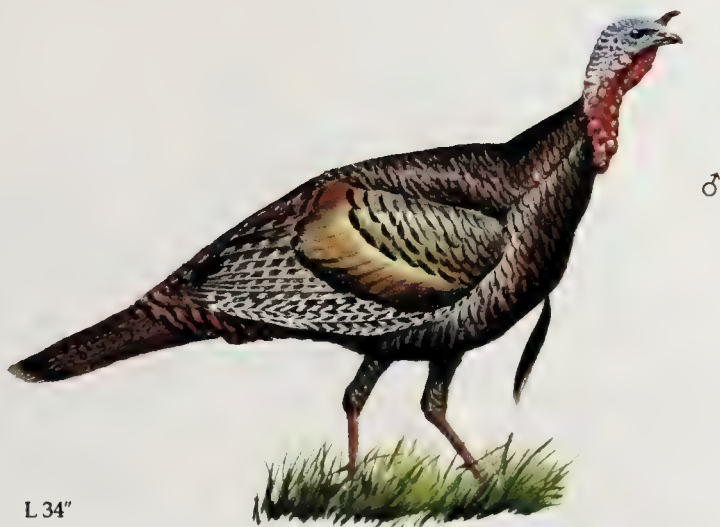
NEST: Nests on the ground, preferably among tall, rank grasses, but also in brushy or woody areas if grassland quality is poor. May nest in fields of winter wheat, or in residual cover of warm season grasses on north-facing slopes.

FOOD: Eats wide variety of foods, primarily the leaves, seeds, or buds of plants, and some insects, but also including fruits, cultivated grains, buds and catkins of birch and aspen, and grasshoppers.

REFERENCES: Hamerstrom 1963, Hamerstrom and Hamerstrom 1951, Johnsgard 1973, 1983a, Rogers 1969, Sisson 1976, Tate and Tate 1982.

Wild Turkey

Meleagris gallopavo
(formerly Turkey)



L 34''

RANGE: Resident locally from central Arizona and central Colorado to northern Iowa, central Michigan, southern New Hampshire, and southwestern Maine south to southern Texas, the Gulf Coast, and Florida. Has been reintroduced into much of its former range, and successfully introduced locally in nearly all states outside the historic range.

STATUS: Locally fairly common.

HABITAT: Inhabits a wide range of forest types from the wooded swamps of the eastern and southeastern states to the sparsely wooded flatlands and river bottoms of the southern Great Plains and coniferous forests of the western mountains. In the East, prefers open, mature hardwood forests containing mast-bearing trees such as oaks; in the Southwest, prefers more arid, grass-dominated habitats having open-topped roosting trees, water, and succulent vegetation. In the West, most often associates with ponderosa or montane forests, scrub oaks, and junipers at altitudes of 6,000 to 12,000 feet.

SPECIAL HABITAT REQUIREMENTS: Mast-producing woodlands with forest openings or clearings, large dense conifers or hardwoods for roosting, and water.

NEST: Nests in a slight depression on dry ground, usually in dead leaves at the base of a tree, beneath a bush, or under a log. Generally nests close to strutting grounds and near water. In western mountains, it usually nests on north-facing slopes from 7,000 to 9,500 feet in elevation.

FOOD: Diet is 90 percent plant foods, including mast of oaks, beeches, and pines; fruits; seeds and grains; and greens of grasses and forbs. Also eats roots, tubers, and insects, especially grasshoppers and walking sticks.

REFERENCES: Boeker and Scott 1969, DeGraff et al. 1980, Hillestad 1973, Johnsgard 1975a, Korschgen 1967, Ligon 1946, Lindzey 1967, Markley 1967.

Montezuma Quail

Cyrtonyx montezumae
(formerly Harlequin Quail)



RANGE: Resident, at least locally, from central and southeastern Arizona, southern New Mexico, and extreme southwestern Texas south into Mexico.

STATUS: Locally fairly common.

HABITAT: Inhabits shaded grassy oak canyons, wooded mountain slopes with bunchgrass, and rocky ravines. Seldom goes far from pine-oak woodlands due to dependence on succulent, bulb-producing forbs that grow in pine-oak understory. Heavy grazing tends to reduce bulb-producing forbs, which are replaced by perennials that can provide adequate cover, but not the underground food reserves required during dry seasons.

SPECIAL HABITAT REQUIREMENTS: Ungrazed pine-oak woodlands.

NEST: Conceals nest in a slight depression on the ground, at the base of trees, in grassy meadows, next to boulders, or under shrubs.

FOOD: Coveys typically feed in close groups, digging out bulbs of nutgrasses, wood sorrels, and other plants. Also eats acorns, seeds of legumes, grasses, and pines; fruits of shrubs and trees; and insects. Water is primarily obtained from food.

REFERENCES: Johnsgard 1975a, Leopold and McCabe 1957, Phillips et al. 1964, Terres 1980, Wallmo 1954.

Northern Bobwhite

Colinus virginianus
(formerly Bobwhite)



RANGE: Resident from southeastern Wyoming and central South Dakota to southern Ontario, southern New Hampshire and southern Maine, south through the central and eastern United States to Florida and southern Arizona into Mexico; introduced and established in western North America.

STATUS: Often common to abundant. Masked bobwhite extirpated in southern Arizona but is being reintroduced.

HABITAT: Inhabits open pastures, meadows with abundant weedy growth, and cultivated or fallow agricultural lands with hedgerows and dense brush, near open woodlands; avoids deep woods. In the Southwest, found in brushy canyons and hillsides or on dry grasslands with scattered mesquite and cactus. Prefers to winter in coveys (within several miles of breeding areas) in areas where dense cover of brushy thickets, hedgerows, or brush piles provide protection and abundant food resources.

SPECIAL HABITAT REQUIREMENTS: Open woodlands adjacent to fields and brushy cover. In winter, brushy cover within 150 feet of feeding areas.

NEST: Builds a well-concealed nest on dry ground, usually in a moderately dense stand of herbaceous and grassy vegetation such as goldenrods, panic grasses, cheatgrass, broom sedge, and bluegrass, with scattered shrubs and briars, and patches of bare ground. Prefers areas where standing vegetation is usually less than 20 inches high and upright stems are separate enough for the birds to pass between.

FOOD: Consumes seeds, fruits, buds, and other plant parts that contribute 95 percent of the diet in winter and 70 percent in summer. Eats primarily green plant leaves in spring. Also eats insects that account for the remaining diet.

REFERENCES: DeGraff et al. 1980, Klimstra and Roseberry 1975, Reid and Goodrum 1979, Robel 1969, Rosene 1969, Tate and Tate 1982, Terres 1980.

Scaled Quail

Callipepla squamata



L 8"

RANGE: Resident from south-central Arizona, northern New Mexico, east-central Colorado, and southwestern Kansas south through western Oklahoma, western half of Texas, and into Mexico. Introduced and established in central Washington and eastern Nevada.

STATUS: Common.

HABITAT: Inhabits dry, open country in valleys, plains, or foothills that have a mixture of bare ground, low herbaceous growth, and scattered brushy cover such as mesquite, soapweed, acacias, mimosas, scrub oaks, and other semi-desert shrubs. May be found on rocky, brushy slopes, draws, gullies, canyons, on sand sage grassland, and sometimes on shortgrass plains, pastures, and cultivated fields. If shrub cover is lacking, uses structures such as corrals, feedlots, and buildings for shade, resting areas, and escape cover. Winters in large coveys, usually within 1 1/4 miles from water.

SPECIAL HABITAT REQUIREMENTS: Desert grassland or desert scrub with a minimum of 1 loafing covert per 70 acres, and a source of water.

NEST: Nests in a slight hollow on the ground in a protected and shaded site. The nest may be under shrubs or among grasses, under old machinery or junk, or under overhanging rocks.

FOOD: Feeds primarily on plant seeds, with some fruits and insects.

REFERENCES: Ault and Stormer 1983; Goodwin and Hungerford 1977; Johnsgard 1973, 1975a; Kelso 1937; Schemnitz 1961; Stormer 1981.

Gambel's Quail

Callipepla gambelii



RANGE: Resident from east-central California, southern Nevada, southern Utah, western Colorado, and northwestern New Mexico south to Mexico and the Rio Grande Valley of western Texas.

STATUS: Common.

HABITAT: Inhabits desert scrub dominated by desert hackberry, mesquite, catclaw, buckhorn and cholla cactus; chaparral; and riparian areas; from sea level to elevations above 6,500 feet. Roosts in shrubs or low trees, where shade, brushy escape cover and succulent vegetation are available within about 1500 feet.

SPECIAL HABITAT REQUIREMENTS: Open water or succulent vegetation.

NEST: Nests on the ground in a scratched-out depression, usually well concealed under tall grass, mesquite, sage, or other shrubs. Occasionally nests above ground in woodpiles, rotted stumps, or abandoned nests of thrashers, roadrunners, or cactus wrens.

FOOD: Consumed a diet of 44 percent forb seeds, 14 percent shrub seeds, 5 percent animal foods, 3 percent grass seeds, and 34 percent leafy vegetation in one study. Eats a variety of foods including deer-vetch, filaree, mesquite, paloverde, lupine, white-thorn, mimosa, saguaro, calowrightia, and insects (largely ants.) Eats succulent foods to maintain body moisture.

REFERENCES: Goodwin and Hungerford 1977, Gorsuch 1934, Harrison 1979, Hungerford 1962, Johnsgard 1975a.

California Quail

Callipepla californica



RANGE: Resident from southern British Columbia, Washington, and western Idaho south through most of Oregon, California, and Utah to Baja California. Most populations north of southern Oregon and east of California apparently the result of introductions.

STATUS: Common over most of its range.

HABITAT: Tolerates a relatively broad variety of climates, from cool, wet coastal areas to arid desert. Lives in foothills and valleys where low trees or shrubs have openings of weeds and grass near water; also in coastal scrub, broken chaparral, edges of woodlands, riparian woodland, and on farms, ranches, and parks. Roosts from 15 to 25 feet up in dense growth of trees or shrubs at night; uses brushy thickets during the day for roosting and escape cover.

SPECIAL HABITAT REQUIREMENTS: Brushy cover within 50 feet of feeding areas, and near a source of water.

NEST: Builds nests in a slight depression on the ground or in tall, dense weedy or grassy cover, well concealed at the base of a tree or shrub, near a fallen tree or under a brush pile. Nests often located along fence rows, in road ditches, or in pastures and close to water.

FOOD: Consumes mostly seeds and leafy green vegetation, with only small amounts of animal food in the spring and summer.

REFERENCES: Bevier in Farrand 1983a, Browning 1977, Emlen and Glading 1945, Gutierrez 1979-1980, Leopold 1977, Sumner 1935, Terres 1980.

Mountain Quail

Oreortyx pictus



RANGE: Resident from southwestern British Columbia, western and southern Washington, and central Idaho south through the mountains of California and northern and western Nevada to Baja California.

STATUS: Common.

HABITAT: Inhabits open montane forests with a well-developed brushy understory, steep slopes around edges of mountain meadows, and in logged or burned-over forests, from 1,500 to 10,000 feet. In California, breeds from chaparral up to lodgepole pine forests, preferring areas with much shrubbery and low percent canopy cover. During winter, moves to a lower elevation and occupies a habitat of mixed trees, brush, and herbs that produce mast and seeds.

SPECIAL HABITAT REQUIREMENTS: Water during the breeding season.

NEST: Nests on the ground, in a well-concealed site, often under fallen pine branches, in weeds or shrubs, at the base of large trees, or beside large rocks. Nests are always near water.

FOOD: Forages on the ground and in low shrubs for food. Consumes leaves, flowers, and buds of succulent vegetation; mast; pine seeds; tubers, roots, and bulbs; seeds and fruits; and insects.

REFERENCES: Gutierrez 1979-1980, Johnsgard 1975a, Ormiston 1966, Terres 1980, Verner and Boss 1980.

Yellow Rail

Coturnicops noveboracensis



RANGE: Breeds locally from northwestern Alberta and southern Mackenzie to southern Quebec and New Brunswick south to southern Alberta, North Dakota, southern Wisconsin, southern Ontario, Massachusetts, and Connecticut. Winters from coastal North Carolina south to southern Florida, west along the Gulf Coast to central and southeastern Texas; in Mexico; and locally from Oregon south to southern California.

STATUS: Depending on locality, common, rare, or casual.

HABITAT: Highly secretive; spends most of its time beneath dense, rank vegetation. Inhabits shallow, freshwater, grassy, and sedge marshes and wet meadows. In fall and winter, lives in high margins of fresh and saltwater marshes, savannahs, grainfields, hayfields, and among garden crops.

SPECIAL HABITAT REQUIREMENTS: Marshes or wet meadows.

NEST: Prefers to nest in drier portions of marsh, usually where ground is damp but there is no standing water. Conceals nest in dense clumps of marsh grasses, with surrounding vegetation forming canopy over the nest.

FOOD: Eats small snails, insects, seeds of sedges, grasses, and clover leaves (very little has been reported on food habits).

REFERENCES: Anderson 1977, Devitt 1939, Terres 1980, Walkinshaw 1939.

Black Rail

Laterallus jamaicensis

L 4½"



RANGE: Breeds locally along the Atlantic Coast from New York south to central Florida; on the Gulf Coast in eastern Texas and western Florida; in Kansas, and from California to South America. Winters along the coast of California from the breeding range north to Tomales Bay; in the Imperial and lower Colorado River Valleys of southeastern California; along the Gulf Coast from southeastern Texas east to Florida; and in South America.

STATUS: Locally common.

HABITAT: Inhabits coastal salt marshes, and occasionally inland freshwater marshes and wet meadows. Uses grainfields and hay meadows to some extent. Prefers higher portions of a marsh, where vegetation is rank and dense and the ground is damp. Life history poorly known; spends much of its time under matted grasses in high salt marshes.

SPECIAL HABITAT REQUIREMENTS: Marshes with areas of dense, but not necessarily tall, cover and damp soil.

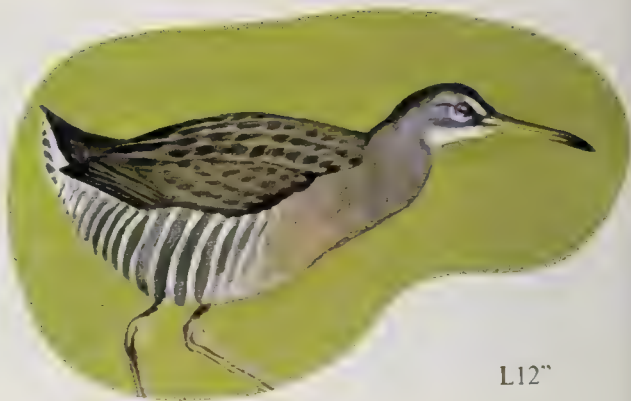
NEST: Completely hides nest in clumps of marsh grass or at the base of glasswort, in or along the edge of a marsh. Usually places nest on matted dead grass, but sometimes directly on damp ground.

FOOD: Probably feeds mainly on invertebrates.

REFERENCES: DeGraff et al. 1980, Pough 1951, Terres 1980, Todd 1977.

Clapper Rail

Rallus longirostris



L12"

RANGE: Resident along the Atlantic and Gulf Coasts from Connecticut south to southern Florida and west to southern Texas; locally along the Pacific Coast from central California south to South America; and in the interior of southeastern California and southwestern Arizona at the southern end of the Salton Sea and in the lower Colorado River Valley (northernmost populations tend to be partially migratory).

STATUS: Abundant in the east, local in California. Some western subspecies are listed as endangered.

HABITAT: Primarily inhabits coastal salt marshes, especially tidal marshes bordered by shallow bodies of salt or brackish water. One subspecies inhabits freshwater marshes along the Colorado River.

SPECIAL HABITAT REQUIREMENTS: Dense growths of cordgrass or needlerush, with deep soft soils.

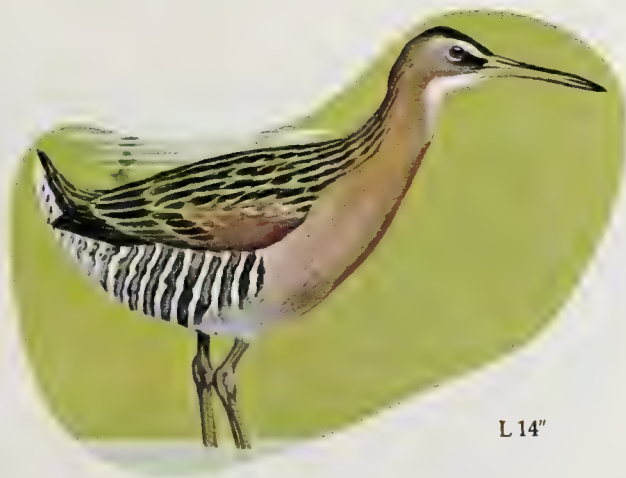
NEST: Builds nest 8 to 12 inches above ground and near water in salt marsh cordgrass, in marsh elder, or other marsh vegetation that is more than 2 feet tall, with a canopy of vegetation. Locates nest so it will not be submerged by high tide.

FOOD: Prefers to feed on mudflats or along muddy shores of creeks at low tide by probing and gleaning. Eats fiddler crabs, other small crabs, crustaceans, snails, shellfish, aquatic insects, and some seeds.

REFERENCES: Adams and Quay 1958, DeGraff et al. 1980, Johnsgard 1975a, Kozicky and Schmidt 1949, Mangold 1977, Stone 1937.

King Rail

Rallus elegans



L 14"

RANGE: Breeds locally from eastern Nebraska and central Minnesota to Connecticut south through northwestern and central Kansas, central Oklahoma, and most of the eastern United States to western and southern Texas, central Mississippi and Alabama, and southern Florida. Winters primarily from southern Georgia, Florida, the southern portions of the Gulf States, and southern Texas south to Mexico.

STATUS: Uncommon; population declining in Midwest prairies, low elsewhere.

HABITAT: Inhabits coastal, and inland brackish and freshwater marshes with abundant vegetation (especially sedges, bulrushes, and cattails), roadside ditches, tidal rivers, ricefields, and upland fields near marshes. Forages and nests along waterways made by the muskrat (distribution coincides closely with that of the muskrat). Not known to breed in salt marshes, but wintering birds inhabit coastal brackish, salt (rarely), and freshwater marshes.

SPECIAL HABITAT REQUIREMENTS: Wetlands with abundant vegetation and fairly stable water levels during the breeding season.

NEST: Conceals nests with a cone-shaped or round canopy of vegetation overhead; usually locates nests 6 to 18 inches above shallow water on grass or sedge tussocks or on hummocks among cattails.

FOOD: Feeds on mud flats at low tide, in open roadside ditches, or in very shallow water, 2 to 3 inches deep. Primarily eats crustaceans, especially crayfish and aquatic insects; also takes grasshoppers, crickets, fishes, frogs, grains (especially rice in winter), and seeds of aquatic plants.

REFERENCES: Bateman 1977, DeGraff et al. 1980, Johnsgard 1975a, Meanley 1969, Tate and Tate 1982.

Virginia Rail

Rallus limicola



L 7½"

RANGE: Breeds locally from southern British Columbia and northwestern Alberta to southern Quebec, New Brunswick, and southwestern Newfoundland south to Baja California, west-central Texas, Kansas, central Ohio, western Virginia, and along the Atlantic Coast to North Carolina; also in central Louisiana and northern Alabama. Winters from southern British Columbia and western Washington south to Baja California; and from central Texas, the Gulf Coast, and coastal North Carolina south locally to Costa Rica; casual in interior North America.

STATUS: Common.

HABITAT: Inhabits freshwater marshes, marshy borders of lakes and streams, and occasionally brackish and salt marshes. Prefers areas with shallow water and abundant emergent vegetation.

SPECIAL HABITAT REQUIREMENTS: Wetlands with sedge and cattail edge.

NEST: Usually constructs nests in cattails or sedges a few inches above shallow water, that are often covered with a loose canopy of vegetation and well attached to surrounding vegetation or on a clump of grass or tussock.

FOOD: Consumes a diet that is about two-thirds insects. Also eats small fishes, frogs, mollusks, crustaceans, leeches, and earthworms. Climbs easily on reeds and in bushes to reach seeds and berries, and also eats grass seeds, duckweeds, wild oats, and rice.

REFERENCES: Berger 1951, DeGraff et al. 1980, Horak 1970, Johnsgard 1975a, Low and Mansell 1983, Walkinshaw 1937, Zimmerman 1977.

Sora

Porzana carolina



L 6¾"

RANGE: Breeds from southern Yukon and west-central and southwestern Mackenzie to west-central and southern Quebec and southwestern Newfoundland, south locally to Baja California, central Arizona, New Mexico, central Illinois, and Maryland. Winters from central California to the Gulf Coast and southern South Carolina south to South America; occasionally north to southern Canada.

STATUS: Common.

HABITAT: Prefers freshwater marshes, but also inhabits brackish and salt marshes, ponds, swamps, bogs, wet grassy meadows, and sloughs, especially those with sedges and cattails. In late summer, concentrates in areas where food is plentiful such as in rice fields or other seed-producing areas.

SPECIAL HABITAT REQUIREMENTS: Wetlands with abundant, dense vegetation.

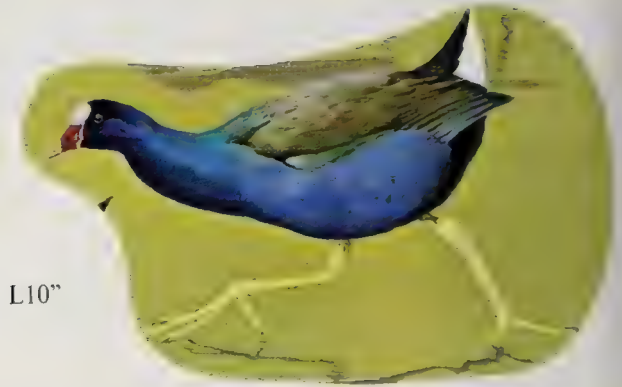
NEST: Constructs a well-concealed nest that may be fastened to or supported by reed stems on a raised platform of vegetation. Locates nest 6 inches to over a foot above water, or occasionally on the ground. Generally nests over water 6 to 8 inches deep, preferably among sedges.

FOOD: Primarily feeds on small mollusks and insects except in the fall; then relies heavily on seeds in freshwater habitats and animal foods in brackish areas. Also eats insects, mollusks, worms, crustaceans, and small tadpoles. Eats seeds and leaves for most of the vegetative portion of the diet.

REFERENCES: DeGraff et al. 1980, Horak 1970, Johnsgard 1975a, Low and Mansell 1983, Meanley 1965, Odom 1977, Walkinshaw 1940, Webster 1964.

Purple Gallinule

Porphyryula martinica



L10"

RANGE: Breeds along the Atlantic Coast from Maryland and Delaware south through Central America to South America, and in eastern and southern Texas, the Gulf States, and Florida; locally in southern Illinois, western Tennessee, and central Ohio. Winters from southern Texas, Louisiana, and Florida south throughout remainder of breeding range.

STATUS: Uncommon throughout breeding range.

HABITAT: Characteristically inhabits marshy wetlands with a variety of marsh plants, especially where pickerelweed and plants with floating leaves, such as water lilies, are abundant. Walks freely on lily pads and other floating vegetation, alights readily on bushes, and climbs about in branches over water.

SPECIAL HABITAT REQUIREMENTS: Freshwater marshes and swamps, ponds, and channels of slow moving water with well-vegetated edges.

NEST: Usually nests on an island of floating water plants. Builds a well-concealed nest, sometimes suspended and woven into marsh vegetation or willow thickets up to 6 feet above shallow water.

FOOD: Consumes both plant and animal foods, including the seeds of rice, duckweed, wild millet, and other aquatic plants; also eats mollusks, aquatic insects, snails, and worms.

REFERENCES: Cramp and Simmons 1980, Holliman 1977, Johnsgard 1975a, Low and Mansell 1983, Terres 1980.

Common Moorhen

Gallinula chloropus
(formerly Common Gallinule)



L10"

RANGE: Breeds locally in California, central Arizona, and northern New Mexico, and from central Minnesota and southern Wisconsin to Vermont and Massachusetts, south to South America. Winters in eastern North America from South Carolina and the Gulf Coast southward, elsewhere throughout the breeding range, occasionally north to Utah, Minnesota, southern Ontario, and New England.

STATUS: Locally common.

HABITAT: Inhabits freshwater marshes, lakes, ponds, slow-flowing streams and rivers, and nearly any body of water with emergent vegetation such as cattails, bulrushes, reeds, sedges, and burreeds growing in water over one foot deep. Also inhabits rice fields in the South.

SPECIAL HABITAT REQUIREMENTS: Emergent vegetation growing in water 1 to 3 feet deep and areas of open water.

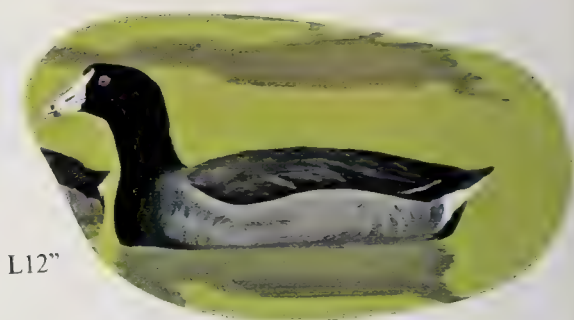
NEST: Builds nests in emergent vegetation 2 to 6 feet high, on a hummock or other clump of vegetation over water that is 1 to 3 feet deep. Locates nest at water level or up to 2 feet above water, concealing it with a canopy of surrounding plants. Occasionally nests in shrubs such as willow or alder. Builds brood platforms or uses muskrat houses or platforms built by coots.

FOOD: Dives, dabbles, or wades while foraging; eats mainly leaves and stems of underwater plants, duckweed, leaves of grasses and herbs, and seeds and berries. Occasionally eats insects, earthworms, slugs, snails, and rarely aquatic vertebrates such as tadpoles or small fishes.

REFERENCES: DeGraff et al. 1980, Fredrickson 1971, Johnsgard 1975a, Krauth 1972, Low and Mansell 1983, Strohmeyer 1977.

American Coot

Fulica americana



L12"

RANGE: Breeds from east-central Alaska and southern Yukon to southwestern Quebec, southern New Brunswick, and Nova Scotia south locally to Central America. Winters from southeastern Alaska and British Columbia south through the Pacific States, and from Colorado and northern Arizona to the lower Mississippi and Ohio Valleys, and Maryland south to the southeastern United States and Central America.

STATUS: Common.

HABITAT: Inhabits marshes, lakes, ponds, sloughs, potholes, and marshy borders of creeks and rivers, or ephemeral habitats when conditions are suitable. Prefers wetlands with a good interspersed of emergent vegetation, especially cattails and bulrushes. During migration, found on rivers, lakes, ponds, reservoirs, or sewage lagoons, and on freshwater or brackishwaters in winter.

SPECIAL HABITAT REQUIREMENTS: Freshwater wetlands, with shallow water 1 to 4 feet deep and emergent vegetation interspersed with areas of open water.

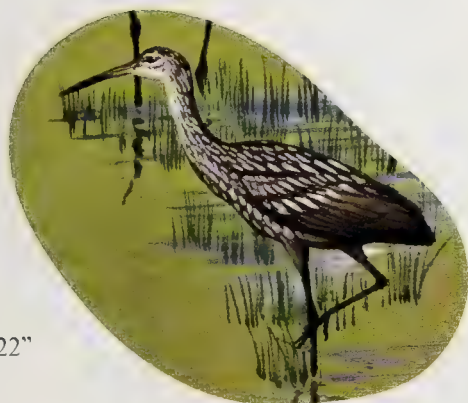
NEST: Constructs floating display platforms, egg nests, and brood nests located in and anchored to emergent vegetation, usually within 4 feet of open water and over water 1 to 4 feet deep. May also nest on top of a muskrat house.

FOOD: Primarily dabbles and grazes, but also dives. Eats a variety of plant foods, which make up 89 percent of the diet. During winter often grazes on pastures and cultivated fields. Eats mostly pondweeds, sedges, algae, grasses (especially wild rice), and other plants; also eats fishes, tadpoles, worms, crustaceans, spiders, beetles, dragonflies, and bugs.

REFERENCES: Cramp and Simmons 1980; DeGraff et al. 1980; Fjeldsa 1977; Fredrickson 1970, 1977; Gullion 1954; Johnsgard 1975a; Jones 1940; Kiel 1955.

Limpkin

Aramus guarauna



L22"

RANGE: Resident from southeastern Georgia and northern Florida (east of the Apalachicola River) south through peninsular Florida, Central America, and South America.

STATUS: Locally common.

HABITAT: Inhabits freshwater cypress swamps, marshes of saw grass or bulrushes, bayous, sloughs, and wooded marshy rivers or streams. Sometimes perches in tops of the tallest trees or on shrubs.

SPECIAL HABITAT REQUIREMENTS: Freshwater marshes with dense vegetation or trees and shrubs for nesting.

NEST: Commonly nests among clumps of tall grasses or other aquatic plants above shallow water. Sometimes nests 5 to 8 feet above the ground in bushes, vines, or trees along banks of streams, or on platforms just above water in dense vegetation.

FOOD: Probes for food in shallow water or in soft mud on mud flats for freshwater snails, especially Pomacea; also eats mussels, frogs, lizards, worms, insects, and a few seeds.

REFERENCES: Bent 1926, Harrison 1975, Oberholser 1974a, Sykes in Farrand 1983a, Terres 1980.

Sandhill Crane

Grus canadensis



L37"

RANGE: Breeds from western and central Alaska and northern Yukon to Baffin Island, south locally to southern Alaska, northeastern California, Colorado, southern Minnesota, southern Michigan, and western Quebec. Resident from southern Mississippi, southern Alabama, and southern Georgia south to Florida. Winters from central California and southeastern Arizona to the Gulf Coast and southern Georgia south to Mexico.

STATUS: Northern subspecies (Lesser, Canadian, and Greater) are migratory and locally common, while nonmigratory subspecies (Cuban, Florida, and Mississippi) are threatened or endangered.

HABITAT: Inhabits prairies, tundra, open pinewood flats, and other open areas. Breeds in or near shallow marshes, bogs, sloughs, margins of lakes, ponds, and river deltas. In mountainous regions, inhabits isolated, well-watered river valleys, marshes, and meadows. Occasionally inhabits relatively small marshes and patches of prairie in forested country. During winter, roosts in flocks at night on low damp ground or in shallow water, and flies to feeding grounds at dawn.

SPECIAL HABITAT REQUIREMENTS: Shallow wetlands adjacent to a meadow, cultivated fields, or open woodlands and free of human disturbance.

NEST: Usually nests in or near shallow wetlands adjacent to feeding grounds. Nests are located on a mound of emergent vegetation, sticks, grass, moss, or mud among rushes, sedges, grasses or other tall, dense vegetation. Pairs mate for life.

FOOD: Feeds in cultivated fields, pastures, wet meadows, and marshes. Eats wheat, corn, alfalfa, sorghum, barley, roots and tubers, berries, small mammals, snakes, frogs, lizards, crickets, and grasshoppers.

REFERENCES: Archibald in Farrand 1983a, Cramp and Simmons 1980, Johnsgard 1975a, Lewis 1977, Terres 1980, Walkinshaw 1949.

Whooping Crane

Grus americana



RANGE: Breeds in the vicinity of Wood Buffalo National Park in south-central Mackenzie and in northern Alberta. Introduced at Grays Lake National Wildlife Refuge, Idaho. Winters in the vicinity of Aransas National Wildlife Refuge on the Gulf Coast of Texas, occasionally northeast to southern Louisiana.

STATUS: Endangered, numbering fewer than 150 individuals in the traditional wild flock, about 13 in the introduced Rocky Mountain flock, and about 55 in captivity.

HABITAT: Inhabits marshy areas interspersed with shallow potholes having soft marly bottoms and a pH range of 7.6 to 8.3. Primarily inhabits aspen parkland, but also in northern coniferous forest, shortgrass plains, northern mixed forest, river deltas, and tundra. Winters on tallgrass prairies, salt flats, coastal marshes, lagoons, and brackishwater areas.

SPECIAL HABITAT REQUIREMENTS: Large, shallow wetlands that provide visibility over a wide area and are free of human disturbance.

NEST: Nests on a mound of bulrushes in shallow water, on islands or along shores of large wetlands where there is a heavy cover of bulrushes. Pairs mate for life, and return to the same general area each year but not to the same nest site.

FOOD: In winter, primarily feeds on blue crabs, but also eats aquatic insects, freshwater minnows, shrimps, crayfishes, marine worms, snails, clams, sprouting corn, acorns, grasses, sedges, and other plants. (Foods of other seasons have not been well documented.)

REFERENCES: Allen 1952, Archibald in Farrand 1983a, Mackenzie 1977, McNulty 1966, Novakowski 1966, Terres 1980.

Black-bellied Plover

Pluvialis squatarola



RANGE: Breeds from northern Alaska south to western Alaska, and from northwestern Mackenzie and Banks Island, southern Melville, Devon, and western and southern Baffin Islands south to the Yukon River, north-central Mackenzie, northern Keewatin, and Southampton and Coats Islands. Winters primarily in coastal areas from southern British Columbia and New Jersey south along both coasts of the United States to South America.

STATUS: Common.

HABITAT: Breeds on moist to dry upland rolling tundra. In other seasons frequents mudflats, beaches, shores of ponds and lakes, flooded fields, and salt marshes. Commonly associates with other shorebirds, especially willets, golden plovers, knots, and curlews.

SPECIAL HABITAT REQUIREMENTS: Tundra during breeding season.

NEST: Nests in a depression on the ground in relatively dry sites on or near a ridge, often in a prominent area affording a wide view. Usually locates nest on gravelly ground, sometimes with large boulders or with sparse vegetation of lichens, dryad, saxifrage, willows, sedges, or grasses.

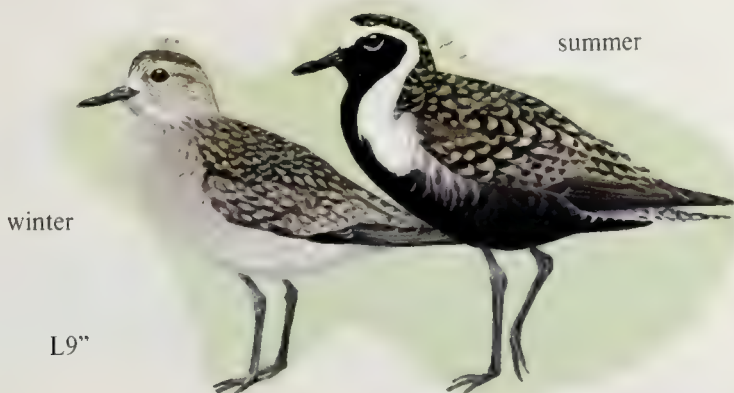
FOOD: Feeds along seacoasts on broad tidal sand flats and mud flats and in salt marshes, or inland around lakeshores, in meadows and upland pastures, or in plowed fields. Diet includes marine worms, small mollusks, crustaceans, marine insects, grasshoppers, locusts, cutworms, grubs, beetles, earthworms, and some seeds and berries.

REFERENCES: Bent 1929, Hussell and Page 1976, Palmer 1967, Terres 1980.

Lesser Golden-Plover

Pluvialis dominica

(formerly American Golden Plover)



RANGE: Breeds from northern Alaska and northern Yukon to Banks, Devon, and northern Baffin Islands south to central Alaska, northwestern British Columbia, southern Keewatin, northern Ontario and Southampton, and southern Baffin Islands. Winters in southern South America.

STATUS: Common, once abundant; population decline due to hunting at the end of the 19th century but is recovering.

HABITAT: Breeds on arctic and subarctic tundra beyond treeline, usually where the ground cover is lichens and mosses. In migration, occupies short-grass pastures, plowed fields, and burned-over meadows, or beaches and mudflats in coastal areas.

SPECIAL HABITAT REQUIREMENTS: Dry, grassy tundra.

NEST: Nests in a depression on dry ground, preferably on higher sites such as banks of gullies or streams but not necessarily near water. Eggs are difficult to see against tundra. Young birds quickly move to wetter areas such as sphagnum swamps.

FOOD: Feeds in rolling pasturelands with short, scanty grass, on prairies, plains, plowed land, open sand, or mud flats. Mostly eats insects, especially grasshoppers and crickets. Also eats grubs, cutworms, caterpillars, beetles, spiders, mollusks, small crustaceans, small fishes, crowberries, and blueberries.

REFERENCES: Bent 1929, Cramp and Simmons 1983, Palmer 1967, Terres 1980.

Snowy Plover

Charadrius alexandrinus



RANGE: Breeds along the Pacific Coast from southern Washington to Baja California, and locally from southern Oregon, western Nevada, southwestern Montana, central Kansas, and north-central Oklahoma south to southeastern California and north-central Texas; also along the Gulf Coast from Florida west to Texas. Winters on islands and in coastal areas from northern Oregon and the Gulf Coast south to Costa Rica.

STATUS: Locally common; suffering a serious decline in the southern and middle Pacific Coast regions.

HABITAT: Inhabits dry sandy coastal beaches above the wash of the tides, sand spits or bars separating the ocean from coastal wetlands, estuarine margins, alkali flats, dry lake beds, or the shores of salt ponds and alkali lakes. Prefers open habitats; avoids thick vegetation and narrow beaches littered with driftwood or backed by bluffs where it might be trapped by high water.

SPECIAL HABITAT REQUIREMENTS: Open nesting habitat, preferably near water.

NEST: Nests singly or sometimes in loose colonies in flat areas devoid of, or sparsely covered with, vegetation or driftwood. Generally nests near water, but occasionally farther away if no formidable barrier is between the nest and water, in a scrape on the ground, usually among small rocks, kelp, or other objects.

FOOD: Forages on wet sand of beaches, at the surf line, or along muddy or alkaline shores of ponds and lakes inland. Food is mostly small crustaceans, marine worms, other minute marine animals, beetles, flies, and other insects.

REFERENCES: Bent 1929, Harrison 1979, Page and Stenzel 1981, Palmer 1967, Tate and Tate 1982, Terres 1980, Wilds in Farrand 1983a.

Semipalmated Plover

Charadrius semipalmatus



RANGE: Breeds from northern Alaska, northern Yukon, Banks, Victoria and central Baffin Islands to the northern Labrador Coast, south to western Alaska, southwestern and central British Columbia, northern Manitoba, central Quebec, and southern Nova Scotia. Nonbreeding birds often summer in the wintering areas south to Panama. Winters primarily in coastal areas from central California, the Gulf Coast, and South Carolina south to South America.

STATUS: Common.

HABITAT: Found during spring and fall migration on beaches, mudflats, lakeshores, riverbanks, freshly plowed fields, shallow marshes, and peat banks. It breeds in dry Arctic tundra, sometimes quite far from water, and prefers lichen-grown gravelly tundra or areas of rubble and patches of stranded debris. Avoids grassy areas.

SPECIAL HABITAT REQUIREMENTS: Level, well-drained gravelly tundra.

NEST: Nests in unsheltered scrapes on level ground in gravelly or sandy soil, or in moss or lichens and above the high-water line in loose colonies.

FOOD: Prefers to feed in shallow streams or mudbars in tundra ponds, but also forages on tidal flats. Diet includes marine worms, mollusks, small crustaceans, larvae of midges and other insects, ants, beetles, grasshoppers, and spiders.

REFERENCES: Cottam and Hanson 1938, Palmer 1967, Sutton and Parmelee 1955, Terres 1980.

Piping Plover

Charadrius melodus



RANGE: Breeds locally from south-central Alberta to south-central Manitoba, south to eastern Montana and central and eastern Nebraska; in the Great Lakes region from northern Michigan and southern Ontario south to the southern shores of Lake Michigan and Lake Ontario; and in coastal areas from Newfoundland south to Virginia. Winters on the coast from South Carolina south to Florida and west to eastern Texas, sparsely in Bahamas and Greater Antilles.

STATUS: Endangered; numbers are slowly declining.

HABITAT: Inhabits exposed, sparsely vegetated sandy shores and islands of shallow lakes and ponds, dry sandy ocean beaches, higher portions of strand near dunes, and large open sandy areas, especially where scattered grass tufts are present. In winter it is found on beaches, margins of lagoons, and areas of rubble.

SPECIAL HABITAT REQUIREMENTS: Unspoiled, undeveloped beaches with little vegetation.

NEST: Nests in a hollow in sand, well beyond high tide on ocean beaches, on raised sandspits, or on the lower slopes of dunes. Generally nests on narrow beaches as little as 6 feet wide. May sometimes nest under tufts of grass. Adults tend to return to the same breeding area year after year.

FOOD: Forages on beaches, along margins of watercourses, and on tidal sandflats for marine worms, insects such as fly larvae and beetles, crustaceans, and mollusks.

REFERENCES: Bent 1929, Cairnes 1982, DeGraff et al. 1980, Harrison 1979, Palmer 1967, Tate and Tate 1982, Terres 1980, Wilcox 1959.

Killdeer

Charadrius vociferus



RANGE: Breeds from east-central and southeastern Alaska and southern Yukon to central Quebec and western Newfoundland, south to Mexico. Winters from southern British Columbia across the central United States to New England and south throughout the remainder of North America to South America.

STATUS: Common throughout range.

HABITAT: Indiscriminately occupies open areas, but favors open dry uplands, meadows, pastures, and disturbed or heavily grazed areas where grass is short, sparse, or absent. In winter, inhabits open fields, beaches, along watercourses, and on mudflats.

SPECIAL HABITAT REQUIREMENTS: Open areas with closely cropped or sparse vegetation.

NEST: Nests in a scrape on gravelly or bare ground, occasionally on a flat or gently sloping roof of a building, often with a few pebbles, grasses, or weeds in the scrape.

FOOD: Prey is snatched or gleaned from the surface of dry or moist ground or from very shallow water. Eats a diet that is mainly insects, especially grasshoppers, beetles, and dragonflies, but also includes centipedes, spiders, worms, snails, crayfish, and weed seeds.

REFERENCES: Cramp and Simmons 1983, DeGraff et al. 1980, Palmer 1967, Terres 1980.

Mountain Plover

Charadrius montanus



RANGE: Breeds from extreme southern Alberta and northern Montana south to central and southeastern New Mexico, western Texas, western Oklahoma, and western Missouri. Winters from central California, southern Arizona, and central and coastal Texas south to Mexico.

STATUS: Common but declining.

HABITAT: A species of the high plains and arid regions of western valleys and hills, usually found far from water. Generally avoids mountainous areas and prefers areas dominated by blue grama grass and buffalo grass. In winter, congregates in flocks of 15 to several hundred on alkali flats, plowed ground, grazed pastures, or other open arid habitats.

SPECIAL HABITAT REQUIREMENTS: Shortgrass prairie and arid plains.

NEST: Nests in scrapes on flat ground, preferably in areas of blue grama-buffalo grass with scattered clumps of cacti and western wheat grass. Avoids tall vegetation.

FOOD: Consumes mostly, if not entirely, insects caught on the dry plains and prairies, primarily grasshoppers, crickets, beetles, and flies.

REFERENCES: Bent 1929, Garrett in Farrand 1983a, Graul 1975, Palmer 1967, Terres 1980.

Black-necked Stilt

Himantopus mexicanus



L13''

RANGE: Breeds locally on the Atlantic Coast from southern New Jersey south to southern Florida, and from southern Oregon, southern Colorado, central Kansas, the Gulf Coast of Texas, and southern Louisiana south to South America. Winters from central California, the Gulf Coast of Texas and Louisiana, and southern Florida south to South America.

STATUS: Common.

HABITAT: Inhabits shallow freshwater and brackish ponds, alkaline lakes, wet meadows, open marshes, and flooded fields and pastures. Commonly associates with other shorebirds, especially avocets, godwits, and curlews.

SPECIAL HABITAT REQUIREMENTS: Shallow wetlands.

NEST: Nests in slight depressions on the ground, on sandy or gravelly shores, or along drier margins of ponds and lakes, or on deep, well-built, floating platforms over shallow water in loose colonies. Also nests on hummocks, on small islands, or under clumps of vegetation and may be well concealed or in the open.

FOOD: Forages along muddy shores and in shallow waters for dragonfly nymphs, caddis flies, mayfly nymphs, flies, billbugs, mosquito larvae, grasshoppers, crayfish, and snails. Also consumes small fishes and seeds of aquatic and marsh plants.

REFERENCES: Bent 1927, Palmer 1967, Terres 1980, Wilds in Farrand 1983a.

American Avocet

Recurvirostra americana



L15"

RANGE: Breeds from southeastern British Columbia and central Alberta to Minnesota, south locally to southern California, northern Utah, and southern New Mexico, and east to central Kansas and coastal Texas. Winters mostly in coastal lowlands from northern California and southern Texas south to Mexico, and locally in southern Florida.

STATUS: Common.

HABITAT: Inhabits the borders of muddy saline, alkaline, and freshwater ponds, lakes, and marshes, particularly favoring shallow alkaline lakes, wet meadows and pastures with scattered open pools. Commonly associates with black-necked stilts, godwits, and lesser yellowlegs.

SPECIAL HABITAT REQUIREMENTS: Wetlands bordered by open flats or areas with scattered tufts of grass.

NEST: Eggs are laid in a scrape on the ground. Nests in colonies on dry, sun-baked mudflats, near water, on low, gravelly or sandy islands with scant vegetation, or in marshes bordering shallow lakes. If the water level rises to flood the nest, adds vegetation to raise the nest above the level of water.

FOOD: Gathers food by stirring up water for seeds, aquatic insects, and small crustaceans, and by probing in soft mud. Consumes dragonfly nymphs, back swimmers, water boatmen, beetles, grasshoppers, crickets, weevils, flies and their larvae, centipedes, small snails, small crustaceans, small fishes, and seeds of marsh and aquatic plants.

REFERENCES: Bent 1927, Gibson 1971, Harrison 1979, Low and Mansell 1983, Palmer 1967, Terres 1980, Wilds in Farrand 1983a.

Greater Yellowlegs

Tringa melanoleuca



RANGE: Breeds from southern Alaska, southwestern Mackenzie, and south-central British Columbia east across the northern and central portions of the Canadian Provinces to central and southern Labrador, Newfoundland, and northeastern Nova Scotia. Nonbreeding birds sometimes summer on the wintering grounds, especially along the coasts of the United States. Winters from Oregon and southern Nevada to southern Texas, the Gulf Coast, and coastal South Carolina south to South America.

STATUS: Common.

HABITAT: Found in the Nearctic boreal region to the edge of subarctic coniferous forest zone, where it inhabits swampy muskegs or bogs with scattered trees, wet clearings and pools, or tundra. Perches freely when breeding, often alighting on tops of trees, bushes, or dead stubs. Outside the breeding season, frequents shallow fresh, brackish, and salt waters, mudflats, river bars, tidal marshes and pools, rain pools in fields, and damp grassy meadows.

SPECIAL HABITAT REQUIREMENTS: Muskeg and tundra.

NEST: Nests in a depression on the ground, usually near trees, logs, or stumps, on a dry wooded ridge or on recently burned ground, and normally near water.

FOOD: Feeds by picking, snatching, skimming, and sweeping, but not by probing. Favors mudflats and shallow borders of lakes and streams for feeding sites, where it finds small fishes, tadpoles, worms, mollusks, snails, crabs, and insects and their larvae.

REFERENCES: Cramp and Simmons 1983, Low and Mansell 1983, Palmer 1967.

Lesser Yellowlegs

Tringa flavipes



RANGE: Breeds from central Alaska and central Yukon to northern Manitoba, northern Ontario, and extreme west-central Quebec south to east-central British Columbia, across to southeastern Manitoba. Winters along the Pacific and Atlantic Coasts from southern California and South Carolina south to South America.

STATUS: Common.

HABITAT: Inhabits the Nearctic coniferous forest zone, from boreal and subarctic regions into the low Arctic; occurs mainly inland, and to some extent upland. Prefers grassy meadows and bogs, natural clearings, or burned areas in forest with scattered stumps and fallen logs, often far from open water. Outside the breeding season, inhabits shallow prairie sloughs in open country, muddy shores of lakes and marshy ponds, sewage beds, river margins, and inland and coastal marshes.

SPECIAL HABITAT REQUIREMENTS: Tundra and muskeg.

NEST: Nests in a depression on the ground, singly or in loose colonies. Locates nest on a dry sloping bank, ridge, or level plateau, in open high woodland with sparse, fairly low undergrowth, in swampy muskeg, or on undrained land surrounded by farmland.

FOOD: Forages by picking and snatching food from shallow water, especially in wet, shortgrass marshes, or in shallow ponds, wet cultivated fields, or on mudflats. Eats ants, bugs, flies, grasshoppers, insect larvae, small fishes, crustaceans, and worms.

REFERENCES: Bent 1927, Cramp and Simmons 1983, Low and Mansell 1983, Palmer 1967.

Solitary Sandpiper

Tringa solitaria



RANGE: Breeds from central and south-coastal Alaska and northern Yukon to northern and central Ontario, east through central Quebec to central and southern Labrador, and south to northwestern and central British Columbia across to southern Manitoba and northern Minnesota. Winters from the Gulf Coast, southeastern Georgia, and Florida south to South America.

STATUS: Common.

HABITAT: Inhabits inland muskeg with scattered mature trees or clumps of trees near freshwater lakes and ponds in the coniferous forest belt of boreal and subarctic regions. On its breeding range it perches freely on treetops, twigs, limbs, and stumps. Outside of the breeding season it occurs inland along shallow freshwater woodland streams, ponds, bogs, flooded marshes, stagnant pools, mudflats, and barnyard puddles.

SPECIAL HABITAT REQUIREMENTS: Muskegs.

NEST: Nests up to 43 feet above ground in the old nests of American robins, waxwings, rusty blackbirds, and eastern kingbirds. Usually uses nests in coniferous trees that border muskeg or open bogs, or beside a lake.

FOOD: Forages while walking about on stranded vegetation, in soft mud, or in very shallow water. Eats aquatic insects, especially larvae, also worms, grubs, dragonfly nymphs, water-scavenger beetles, water boatmen, grasshoppers, caterpillars, spiders, small crustaceans, and small frogs.

REFERENCES: Bent 1929, Cramp and Simmons 1983, Palmer 1967, Pough 1951.

Willet

Catoptrophorus semipalmatus



RANGE: Breeds locally from eastern Oregon, central Alberta, and southwestern Manitoba, south to northeastern and east-central California, across to western and northern Nebraska and eastern South Dakota; locally along the Atlantic and Gulf Coasts from Prince Edward Island south to southern Florida and west to southern Texas. Occurs sporadically (nonbreeding birds) in summer as far south as northern South America. Winters along the Pacific and Atlantic Coasts from northern California and Virginia south to South America.

STATUS: Common.

HABITAT: Inhabits tidal and coastal marshes, beaches, sandy islands with tall and thick grasses, open pastures, dry uplands near water, and along dunes in the East. Prefers inland prairies and plains, alkali flats, and grassy dikes, usually near water in the West. Associates freely with godwits, curlews, large plovers, and some shorebirds. Often perches on bushes, trees, fences, posts, rocks, and buildings.

SPECIAL HABITAT REQUIREMENTS: Moist plains and prairies in western North America, coastal marshes and nearby grassy areas in the East.

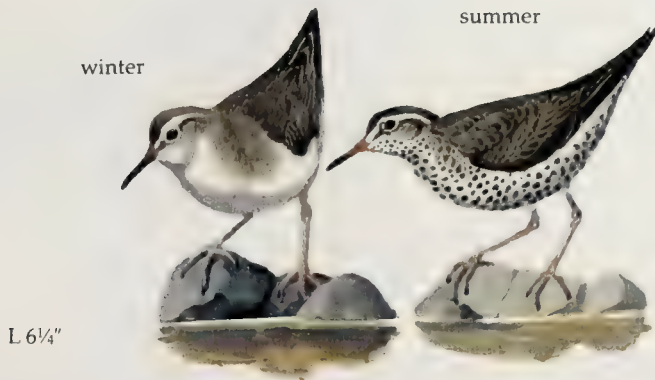
NEST: Nests semi-colonially in depressions on the ground or in a thick clump of vegetation, sometimes far from water in the West. Locates nest in open areas on a sandy beach to well hidden in low grasses.

FOOD: Forages by probing or by snatching food from the ground on tidal flats, in salt or brackish marshes, water-soaked pastures, along muddy creek banks, and on saline flats. Eats fiddler crabs, mollusks, marine worms, small fishes, adult insects, and some seeds, leaves, and roots of grasses.

REFERENCES: Bent 1927, Low and Mansell 1983, Palmer 1967, Stenzel et al. 1976, Terres 1980, Wilds in Farrand 1983a.

Spotted Sandpiper

Actitis macularia



RANGE: Breeds from central Alaska and central Yukon to Labrador and Newfoundland, south to southern Alaska, southern California, and central Arizona across to the northern portions of the Gulf States, North Carolina, Virginia, and eastern Maryland. Occasionally nonbreeding birds remain on the wintering ground in summer. Winters from southwestern British Columbia, southern Arizona, southern New Mexico, southern Texas, the southern portions of the Gulf States and coastal South Carolina south to South America.

STATUS: Common.

HABITAT: Inhabits the edges of ponds, lakes, rivers, and streams and open terrain with temporary pools, up to 14,000 feet elevation. It is sometimes found far from water in dry fields, pastures, and weedy shoulders of roads, occasionally on coastal beaches and dunes. Roosts on stumps, stranded logs, or rocks affording a clear view. In winter, frequents watercourses shaded by trees, and prefers shallow, muddy lagoons, creeks, canals, and higher mudflats.

SPECIAL HABITAT REQUIREMENTS: Margins of freshwater bodies.

NEST: Builds solitary or loosely colonial nests on the ground, among thick, tall grasses, occasionally under a bush or log, and usually near water.

FOOD: Forages ashore or in shallow water, picking up insects and other small invertebrates. Eats fly larvae, pupae, and adults; mayflies; grasshoppers; crickets; mole crickets; worms; mollusks; crustaceans; and spiders.

REFERENCES: Cramp and Simmons 1983, DeGraff et al. 1980, Knowles 1942, Palmer 1967.

Upland Sandpiper

Bartramia longicauda



L 10"

RANGE: Breeds locally from north-central Alaska, northern Yukon, and northern Alberta to southern Quebec, central Maine, and southern New Brunswick south to northeastern Oregon, central Colorado, north-central Texas, central Missouri, West Virginia, and Maryland. Winters in South America.

STATUS: Uncommon; once abundant, numbers have been reduced due to past hunting pressure and agricultural practices.

HABITAT: Inhabits grassy open areas, ranging from sandy, sparsely vegetated flats to open, grassy bogs and muskeg. Most often found in rich pastureland, hayfields, and alfalfa fields. During the breeding season alights freely fenceposts, telephone poles, and other elevated sites. During migration, frequents alfalfa fields, pastures, prairie dog towns, and rarely shores and mudflats.

SPECIAL HABITAT REQUIREMENTS: Open grasslands.

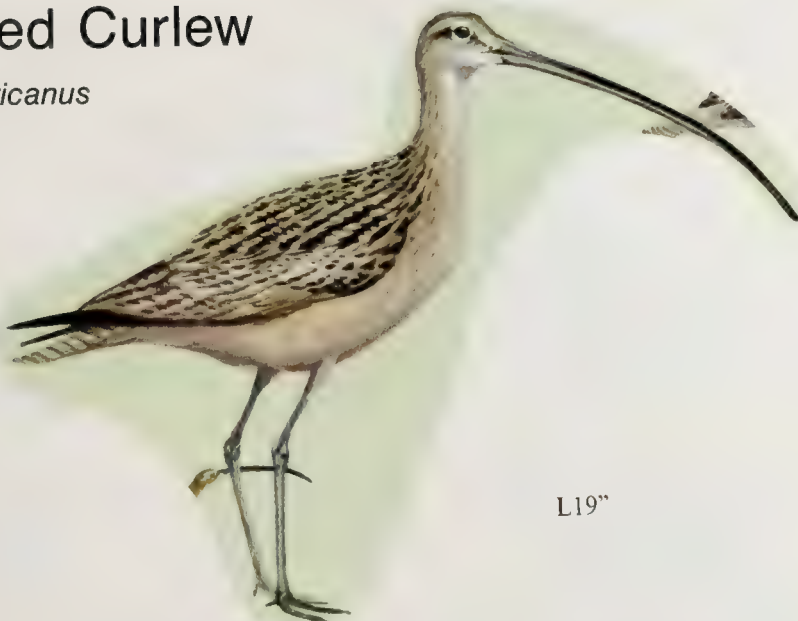
NEST: Nests in depressions on the ground among rank grasses, along sloughs in prairies, or in clearings of spruce muskeg, in loosely spaced colonies. Conceals nests are by covering them with nearby vegetation.

FOOD: Prefers to forage where the grasses are low and open enough to provide good visibility, and where grasshoppers and crickets are most abundant. Also eats weevils, ants, berries, waste grain, and seeds of grasses and weeds.

REFERENCES: Cramp and Simmons 1983, DeGraff et al. 1983, Palmer 1967, Tate and Tate 1982.

Long-billed Curlew

Numenius americanus



L19"

RANGE: Breeds from south-central British Columbia to southern Manitoba, south to northeastern California, central Utah, central New Mexico, and northern Texas, and east to southwestern Kansas. Winters from central California, southern Texas, southern Louisiana, and coastal South Carolina south to Mexico.

STATUS: Fairly common; once fairly abundant, lower population is due to past hunting pressure and loss of habitat due to grazing and agriculture.

HABITAT: Inhabits grasslands ranging from moist meadowland to very dry prairie. When at or near water, often loosely associates with godwits, willets, and yellowlegs. During the breeding season, commonly perches on bushes, low trees, dirt mounds, rocks, stumps, fenceposts, utility poles, or on other elevated sites. In other seasons, frequents wet habitats such as the shallow margins of inland and coastal waters, open areas of marshes, intertidal zones, or on sandbars.

SPECIAL HABITAT REQUIREMENTS: Prairies or grassy meadows.

NEST: Nests in a slight hollow on the ground, usually in flat areas among short grasses such as cheatgrass and bluegrass. Locates nests in moist or arid areas far from water.

FOOD: Forages in areas that have a large variety of plants. Feeds by probing and pecking in wet sand or mud, under shallow water, or in uplands. Eats beetles, grasshoppers, caterpillars, other insect larvae, mud crabs, fiddler crabs, ghost shrimps, occasionally small fishes, and berries.

REFERENCES: Allen 1980, Palmer 1967, Stenzel et al. 1976, Tate and Tate 1982.

Hudsonian Godwit

Limosa haemastica



RANGE: Breeds locally in south-coastal and western Alaska, Mackenzie, northwestern British Columbia, and around Hudson Bay. Winters in South America.

STATUS: Locally common.

HABITAT: Inhabits wet bogs and marshes in open expanses along the northern edge of boreal forests and moist tundra, near tidal or fluvial shorelines. In other seasons, frequents fresh, brackish, and salt waters, on beaches, mudflats, marshes, flooded fields, and shallow ponds.

SPECIAL HABITAT REQUIREMENTS: Extensive sedge marshes and meadows near tidal flats.

NEST: Nests in a depression on top of a hummock in a sedge marsh or meadow with water up to several inches deep. Frequently locates nest under a dwarf birch, occasionally on a sedge or grass tussock, under or among small willows, or near a fallen spruce tree, but usually where the vegetation is at least 5 to 6 inches high and thick enough to conceal the nest from the sides.

FOOD: Feeds on marine worms, horseflies, mosquitoes, and other insects, mollusks, and crustaceans. Prefers to feed in water about as deep as its bill is long.

REFERENCES: Bent 1927, Hagar 1966, Mackenzie 1977, Palmer 1967, Wilds in Farrand 1983a.

Marbled Godwit

Limosa fedoa



L16"

RANGE: Breeds from central Alberta to southern Manitoba and northern Ontario south to central Montana, northeastern South Dakota, and northwestern Minnesota. Some nonbreeding birds occur on the winter range during summer. Winters from central California, western Nevada, the Gulf Coast and coastal South Carolina south to South America.

STATUS: Common.

HABITAT: Inhabits grassy plains, broad flat wet meadows, and prairie sloughs, usually near lakes, rivers, or streams. During migration, frequents open coastal beaches and along lake shores; in winter, inhabits tidal flats in sheltered bays, next to inlets, and on open beaches. Gregarious and often in the company of willets and avocets.

SPECIAL HABITAT REQUIREMENTS: Grassy prairies near water.

NEST: Builds single, or possibly semi-colonial, nest in slight hollow in short grasses, often in plain sight and usually near water.

FOOD: Forages by probing in shallow water and soft mud of sloughs and lake shores for aquatic insects and mollusks, and by capturing grasshoppers and other insects on meadows and low-lying prairies. Also eats snails, small crustaceans, insect larvae, worms, and leeches.

REFERENCES: Bent 1927, Palmer 1967, Wilds in Farrand 1983a.

Ruddy Turnstone

Arenaria interpres



RANGE: Breeds from northern Alaska and the Canadian Arctic islands south to western Alaska, and Southampton, Coats, and Mansel Islands, probably also the northern portions of Mackenzie and Keewatin. Nonbreeding birds may be found through the winter range in summer. Winters along the Pacific and Atlantic Coasts from central California and New York south to South America.

STATUS: Common.

HABITAT: Inhabits flat, lichen-covered, mossy, or gravelly tundra near the seacoast in a variety of boreal habitats. Often perches on boulders, stakes, pilings, piers, and boats during breeding season. In other seasons, frequents rocks, reefs, and mussel beds of the intertidal zone, sandy beaches, and solid mudflats.

SPECIAL HABITAT REQUIREMENTS: Dry, dwarf-shrub tundra near the coast.

NEST: Nests in a depression in tundra in exposed or sheltered sites such as beside a rock or clump of vegetation. Uses a wet area near the nest site for brood rearing.

FOOD: Forages among seaweeds, rocks and shells, and roots in wet sand. Eats mollusks, crustaceans, worms, flies and their larvae picked from the carcasses of seals and whales, eggs of gulls and terns, grasshoppers, soft parts of barnacles, sand fleas, and fiddler crabs.

REFERENCES: Bent 1929, Palmer 1967, Terres 1980, Wilds in Farrand 1983a.

Red Knot

Calidris canutus



RANGE: Breeds in northwestern and northern Alaska and the Canadian Arctic islands east to Ellesmere Island and south to southern Victoria and Southampton Islands. Nonbreeding birds occasionally summer in the wintering range. Winters along the Pacific and Atlantic Coasts from southern California and Massachusetts south to South America.

STATUS: Locally common; once abundant, its numbers were reduced by hunting in the late 19th century.

HABITAT: Inhabits high inland plains, plateaus, and elevated slopes covered with glacial gravel and frost-riven rocks and shales, sometimes several miles from the coast. In migration and in winter, occurs mainly along the coast on exposed mudflats, sand spits, beaches, matted salt marshes, and river deltas.

SPECIAL HABITAT REQUIREMENTS: Barren or stony tundra and dry nesting sites.

NEST: Nests in a shallow depression among dryads, lichens, and other tundra vegetation, rubble, and gravel, and usually on high, dry hills and plateaus.

FOOD: Flies to fresh waters or marine shores from nesting areas up to several miles away to feed during the breeding season. Mainly feeds on the surface, but also probes for food in mud and sand. Eats insects, mollusks, crustaceans, king crab eggs, and some seeds, buds and shoots of grasses, sedges, pondweeds, and bulrushes.

REFERENCES: Bent 1927, Davis in Farrand 1983a, Palmer 1967, Sperry 1940, Terres 1980.

Sanderling

Calidris alba



RANGE: Breeds in northern Alaska, and from Prince Patrick Island to northern Ellesmere Island, south to northern Mackenzie, northern Keewatin, and Southampton, and northern Baffin Islands. Nonbreeding birds occur in summer in the winter range. Winters in the Aleutian Islands (locally), and from southern Alaska, the Gulf Coast, and Massachusetts south along the Atlantic and Pacific Coasts to South America.

STATUS: Common.

HABITAT: Inhabits high Arctic tundra, particularly dry clay-mixed stony plains sparsely covered with willows, dryad, and saxifrage, on islands, peninsulas, and along the coast. Outside the breeding season, frequents sandy coastal beaches and tidal flats. Inland migrants inhabit sandbars along rivers and on lake beaches.

SPECIAL HABITAT REQUIREMENTS: Dry tundra.

NEST: Nests in a slight hollow or depression on the ground on stony, well-drained ridge tops, gentle slopes, or on level alluvial plains. Usually locates nest at the edge of, or in, clumps of low plants and within several hundred yards of a marshy pond, but occasionally nests up to a mile from wet tundra.

FOOD: Probes in wet sand, picks up food washed on shore by the tide, and snatches up insects. In winter and on migration, feeds on sand fleas, shrimp, and other small crustaceans, small mollusks, and marine worms. On the breeding grounds, feeds on flies and their larvae, and other insects.

REFERENCES: Bent 1927, Cramp and Simmons 1983, Davis in Farrand 1983a, Parmelee 1970, Palmer 1967.

Semipalmated Sandpiper

Calidris pusilla



RANGE: Breeds from the Arctic Coast of western and northern Alaska north to Victoria and central Baffin Islands, east to northern Labrador, and south to western Alaska and east-central Mackenzie across to northern Ontario, northern Quebec, and coastal Labrador. Nonbreeding birds may summer in coastal North America south to the Gulf Coast and Panama. Winters from southern Florida south to South America.

STATUS: Abundant.

HABITAT: Inhabits subarctic and low to high Arctic tundra from coasts, dunes, borders of tidal inlets and deltas to damp grassy flats in interior and wet riverside tundra. Often occurs near lakes or pools, shifting from first areas uncovered by melting snow and surface ice to others becoming clear shortly afterwards, including upland tundra. In other seasons, frequents mudflats, sandy beaches, and wet meadows, favoring the vicinity of water on tidal flats, lagoons, and ponds.

SPECIAL HABITAT REQUIREMENTS: Grassy or hummocky tundra.

NEST: Nests in a slight depression on the ground, amid short herbage, sometimes in sand on grassy dunes or in low wet tundra near small lakes.

FOOD: Forages by snatching food from surface and probing in soft mud on mudflats or in wet sand exposed by ebbing tide. Eats beetles, flies, fly larvae, mosquitoes, small mollusks, marine worms, small crustaceans, and bits of seaweeds.

REFERENCES: Cramp and Simmons 1983, Davis in Farrand 1983a, Palmer 1967, Terres 1980, Townsend in Bent 1927.

Western Sandpiper

Calidris mauri



RANGE: Breeds on islands in the Bering Sea and along the coasts of western and northern Alaska. Winters from California and North Carolina south along both the Pacific and Atlantic Coasts to South America.

STATUS: Common.

HABITAT: Inhabits a complex mosaic of wet low-lying grass and sedge marshes dotted with small pools and lakes, and relatively well-drained heath-covered tundra such as hummocks, ridges, and better drained slopes of hills that are vegetated with mosses, lichens, dwarf shrub heath, dwarf birch, willows, and some herbs, grasses, and sedges. Outside of the breeding season, frequents mudflats, beaches, shores of lakes and ponds, and flooded fields.

SPECIAL HABITAT REQUIREMENTS: Patches of dwarf shrub-heath tundra (at least 1/2 acre) interspersed among wet marshes for nesting.

NEST: Nests on the ground in loose colonies or singly in nests that are usually well camouflaged under low vegetation. Locates nests in dry or moist areas, from the upper slopes of hills down to the marsh edge, or within a marsh on a patch of heath tundra. After fledging, moves into the marshes, frequenting margins of lakes and rivers.

FOOD: Feeds by snatching or probing for food close to or in water; eats small invertebrates, including insect larvae and aquatic beetles, bugs, marine worms, and small snails.

REFERENCES: Bent 1927, Cramp and Simmons 1983, Holmes 1971, Palmer 1967.

Least Sandpiper

Calidris minutilla



RANGE: Breeds from western Alaska and northern Yukon to southern Keewatin, northern Quebec, and northern Labrador south to the Alaska Peninsula, southeastern Alaska, and northwestern British Columbia across to northern Ontario, eastern Quebec, Nova Scotia, and Newfoundland; isolated breeding in Massachusetts. Nonbreeding birds summer in the wintering range, primarily in North America south to California and the Gulf Coast. Winters from coastal Oregon and southern Nevada to central Texas, the Gulf States, and North Carolina south to South America.

STATUS: Very common.

HABITAT: Inhabits open grass or sedge bogs and marshes in the northern spruce forest just south of treeless tundra, or among complexes of pools and water channels with scattered knolls and hummocks. Outside of the breeding season, prefers wet, muddy, or grassy areas such as muddy shores of grass fringed marshes or estuaries, grassy wet meadows, and grass-bordered mudflats of lakes, ponds, or rivers; found less frequently on sandy beaches.

SPECIAL HABITAT REQUIREMENTS: Wetlands of subarctic boreal forests and tundra.

NEST: Nests in a depression in a mossy hummock, a plant tuft, in a clump of grass, or sometimes on the ground, usually in marshy cover but sometimes in drier upland near water.

FOOD: Prefers to feed in marshes, where it snatches insects or probes for food in soft mud or in shallow water. Eats midges and other dipterans, ground beetles, grasshoppers, insect larvae, small crustaceans, small mollusks, and worms.

REFERENCES: Cramp and Simmons 1983, Cottam and Hanson 1938, Low and Mansell 1983, Palmer 1967, Pough 1951, Terres 1980.

White-rumped Sandpiper

Calidris fuscicollis



RANGE: Breeds from northern Alaska to northern Bylot Island, south to the mainland coasts of Mackenzie and Keewatin, northwestern Hudson Bay, Southampton Island, and southern Baffin Island. Migrates along the Atlantic Coast and winters in South America.

STATUS: Uncommon.

HABITAT: Inhabits both lowland and upland tundra, frequently around bog pools, on dry ridges, or among grassy tussocks near rivers or lakes. Usually closely associated with moist, open terrain, but tolerates occasional freezing and snow cover and a wide range of temperatures. In migration, prefers shallow grassy pools, wet meadows, and marshes but also occurs on sandbars, mudflats, and beaches.

SPECIAL HABITAT REQUIREMENTS: Mossy or grassy tundra.

NEST: Nests in mossy depressions in clumps of grasses and sedges in the uplands, or in mossy hummocks on well-vegetated tundra that is persistently wet, often near marshy ponds and lake shores. Conceals nest, usually among grasslike plants, including narrow-leaved cotton-grass, grass rush, water sedges, and mosses.

FOOD: Forages by snatching prey and by probing deeply in soft mud. Eats crane fly larvae, beetles, grasshoppers, clover-root curculio, and other insects, tiny mollusks, marine worms, and a few seeds.

REFERENCES: Bent 1927, Cramp and Simons 1983, Drury 1961, Palmer 1967, Parmelee et al. 1968, Terres 1980.

Baird's Sandpiper

Calidris bairdii

L 6"



RANGE: Breeds from western and northern Alaska to Ellesmere Island, south to central Alaska, northern Mackenzie, Keewatin, Southampton Island and south-central Baffin Islands. Winters in South America.

STATUS: Uncommon.

HABITAT: Inhabits dry coastal and alpine tundra, particularly barren, exposed ridges, terrace banks, and raised beaches that are sparsely covered with low matted vegetation. Prefers sheltered places and frequents muddy, sandy, and grassy areas near water, including irrigated fields, shores of lakes and ponds, alpine tundra, and marshes. During migration, prefers inland to coastal habitats.

SPECIAL HABITAT REQUIREMENTS: Dry tundra.

NEST: Nests are in shallow depressions on the ground, usually in wind-blown and lichen-strewn areas with large patches of bare soil. Sometimes nests in grassy areas in a tuft of vegetation or among lichen-covered rocks.

FOOD: Forages by snatching food, primarily in dry areas or along wet edges of lakes and ponds. Eats small crustaceans, spiders, beetles and their larvae, gnats, craneflies, and other insects, moss, leaves and stems, and other plant parts.

REFERENCES: Cramp and Simmons 1983, Davis in Farrand 1983a, Drury 1961, Palmer 1967, Terres 1980.

Pectoral Sandpiper

Calidris melanotos



L 7½"

RANGE: Breeds from western and northern Alaska to Bathurst and Devon Islands, south to western Alaska, central Mackenzie, and southeastern Keewatin Districts, and the south coast of Hudson Bay. Winters in South America, casually north to the Gulf Coast and Florida.

STATUS: Common.

HABITAT: Inhabits dry and moss-lichen tundra, tundra grassland, tussocky tundra with sedge, and peat tundra with hummocks up to 10 to 15 feet. In Alaska, found along the coast and in the foothills, frequenting a variety of tundra habitats on flat terrain that are poorly drained, usually wet, and characterized by low grasses and sedges, dwarf shrubs, and cottongrass tussocks. Outside of the breeding season, prefers grassy terrain bordering moving or still waters; only rarely found on open mudflats.

SPECIAL HABITAT REQUIREMENTS: Dry nesting sites on arctic tundra.

NEST: Nests in a depression on dry ground in areas with a continuous cover of grasses and sedges. Hides nest well, usually under a tree or bush.

FOOD: Forages mainly in dry, grassy meadows on insects, especially flies and their larvae. Also eats beetles, crickets, grasshoppers, amphipods, other tiny crustaceans, mites, spiders, algae, and a few seeds of grasses, lupines, and violets.

REFERENCES: Bent 1927, Cramp and Simons 1983, Low and Mansell 1983, Palmer 1967, Pitelka 1959.

Stilt Sandpiper

Calidris himantopus



RANGE: Breeds from northern Alaska, northern Yukon, northern Mackenzie, and southern Victoria Island southeast to southeastern Keewatin, northeastern Manitoba, and northern Ontario, probably also south locally in Canada to borders of the taiga. Winters primarily in South America, but casually northward to southeastern California, the Gulf Coast, and Florida.

STATUS: Uncommon.

HABITAT: Inhabits sedge meadows interrupted by old beach ridges, eskers, or other elevated areas dominated by dwarf birch, heaths, willows, crowberries, and dryads. Sometimes occurs in wet tundra areas with fairly high willows, or on much drier slopes with moderate vegetative cover, avoiding truly barren ridgetops.

SPECIAL HABITAT REQUIREMENTS: Well-drained sedge meadows in arctic tundra with elevated sites for nesting.

NEST: Nests in a depression on the ground in relatively open areas of dry tundra, usually atop a hummock or on a low, well-drained gravel ridge; occasionally nests next to a shrub. Locates nest sites independent of standing water. May reuse old nests. Moves chicks from drying sedge meadows to wet areas.

FOOD: Forages on dry ridgetops, around clumps of sedges, at the edges of tiny depressions filled with water, in marshes at tundra pond margins, by probing in soft mud on mudflats or while wading in water. Feeds opportunistically, on a relatively small spectrum of food including larval and adult beetles, larvae of other insects, flies and other flying insects, water bugs, small snails, and small seeds.

REFERENCES: Cramp and Simmons 1983, Jehl 1973, Palmer 1967, Terres 1980.

Buff-breasted Sandpiper

Tryngites subruficollis



L 6½"

RANGE: Breeds from northern Alaska to Banks, Melville, Bathurst, and Devon islands, south to northwestern Mackenzie, and Jenny Lind, and King William Islands. Winters in South America.

STATUS: Uncommon; once abundant, its numbers were reduced by several decades of hunting pressure.

HABITAT: Prefers raised and grassy terrain, sometimes by streams, but avoids marshy areas. Predominately a ground bird, it only occasionally occurs on beaches and along shores in migration, favoring short-grass prairies, burned-over grasslands, cotton fields, recently plowed fields, sun-baked stubble, and barren, recently inundated lands.

SPECIAL HABITAT REQUIREMENTS: Dry, grassy tundra.

NEST: Nests in a shallow cavity in dry, mossy or grassy tundra, sometimes near water or on high and dry banks of black tundra.

FOOD: Forages primarily on insects gleaned from the surface. Eats adult and larval beetles, larvae and pupae of flies, some spiders, and seeds of smartweeds, pondweeds, and spikerushes.

REFERENCES: Bent 1927, Cramp and Simmons 1983, Palmer 1967.

Short-billed Dowitcher

Limnodromus griseus



L 9½"

RANGE: Breeds from southern Yukon to northeastern Mackenzie, south to east-central British Columbia, and across to central Saskatchewan; from the interior of the Ungava Peninsula south to northern Ontario, and in coastal regions of southern Alaska. Nonbreeding birds often occur south to wintering grounds in summer. Winters from central California, southern Arizona, the Gulf Coast, and coastal South Carolina south to South America.

STATUS: Common.

HABITAT: Primarily inhabits coniferous forest and muskeg with thin crusts of moss and long grass floating on a liquid morass, but also inhabits swampy coastal tundra. Low scrub of willow, alder, and birch are often present, with a few taller larch and spruce, sometimes flanked by dry ridges of dense coniferous forest or burned-over forests. After breeding, moves to open prairie lakes and sloughs. During migration and winter, occurs on mud and sand flats in sheltered bays and estuaries, on the borders of shallow pools in salt marshes, on sandy beaches, and in flooded fields.

SPECIAL HABITAT REQUIREMENTS: Swampy coastal tundra or muskeg.

NEST: Nests in a hollow in mosses, in a clump of grasses, or on dry ground in wet areas. Sometimes nests in a small clearing in coniferous forest near muskeg, but not under trees or in broken terrain.

FOOD: Feeds by probing deeply in wet sand, mud, in shallow water, or in seaweeds. Eats flies, beetles, dragonfly nymphs, and other insects, as well as marine worms, snails, crabs, shrimps, and seeds of marsh and aquatic plants.

REFERENCES: Cramp and Simmons 1983, Palmer 1967, Sperry 1940.

Long-billed Dowitcher

Limnodromus scolopaceus



RANGE: Breeds in coastal western and northern Alaska, northern Yukon, and northwestern Mackenzie. Winters from central California, southern Arizona, southern New Mexico, central Texas, the Gulf Coast, and southern Florida south to Panama.

STATUS: Common.

HABITAT: Found on arctic continental coastal belts and marginally within the subarctic just beyond treeline. Inhabits grassy and sedgy tundra, with or without scattered low woody vegetation and usually near shallow fresh water. In migration and winter, prefers grassy margins of shallow, muddy freshwater pools and, occasionally saltwater habitats. Associates freely with other shorebirds, including the larger plovers.

SPECIAL HABITAT REQUIREMENTS: Grassy tundra and wet meadows.

NEST: Nests in a shallow depression in a tuft of grass or in moss, on dry or moist ground, usually near freshwater.

FOOD: Feeds in open unvegetated tracts of mud, as well as patches surrounded by tundra. Eats flies, beetles, small crustaceans and mollusks, marine worms, spiders, and seeds of aquatic plants.

REFERENCES: Bent 1927, Cramp and Simmons 1983, Palmer 1967, Sperry 1940.

Common Snipe

Gallinago gallinago



RANGE: Breeds from northern Alaska and northern Yukon to southern Keewatin, northern Quebec, and central Labrador, south to central California, east-central Arizona, and northern Colorado across to northern West Virginia, New England, and the Maritime Provinces. Winters from southeastern Alaska, southern British Columbia, the central United States, and Virginia south to South America.

STATUS: Common.

HABITAT: Inhabits wetlands, especially fens, bogs, swamps, and marshes, primarily in peatlands scattered within the spruce, fir, and larch boreal forest. Occupies areas with fairly dense, low woody growth such as willows and alders, and with a ground cover of sphagnum, sedges, and grasses, preferably near open pastures or other clearings. Also inhabits areas of decomposed wet plant litter along ponds, meandering rivers and brooks, and other marshy sites. In winter it occupies wet, marshy habitats, wet meadows, flooded fields, and stream edges.

SPECIAL HABITAT REQUIREMENTS: Bogs, fens, and swamps with moist organic soils near open areas free of obstacles or high vegetation that might interfere with display activities.

NEST: Nests in a scrape on fairly dry ground or in a tussock of grass or sedge, usually in wet habitats but occasionally at the edge of wetlands. Conceals nest, sometimes covering it with an arch of dry vegetation.

FOOD: Forages by probing in soft mud and shallow water, and by gleaning grasses and the surfaces of marsh plants. Diet consists primarily of animal foods including insects, crayfish, crabs, earthworms, and mollusks. Also eats some seeds.

REFERENCES: DeGraff et al. 1980, Fogarty and Arnold 1977, Palmer 1967, Sperry 1940, Tuck 1972.

American Woodcock

Scolopax minor



L 8¼"

RANGE: Breeds from southern Manitoba, northern Minnesota and south-central and southern Ontario to northern New Brunswick and Newfoundland, south throughout eastern North America to the Gulf States, and southern Florida, and west. Winters from eastern Oklahoma, southern Missouri, Tennessee, and Virginia south to east-central Texas, the Gulf Coast, and southern Florida.

STATUS: Common; may be declining in parts of the East.

HABITAT: Inhabits moist woodlands in early stages of succession especially, those with birch, aspen, red maple, alder, or willows under 25 feet tall and having an understory of conifers. Also found in alder swales with surrounding pockets of second-growth mixed hardwoods, old agricultural fields, burned or recently logged areas, areas too wet to support forest growth, hardwoods adjacent to streams and ponds, and brushy edges of woods. Uses open fields, cultivated land, pastures, and clearings at least 1/4 acre in size on relatively flat ground, and with a slight amount of ground cover for singing grounds.

SPECIAL HABITAT REQUIREMENTS: Dense brushy swales with nearby fields or small forest openings for courtship activities and roost sites, and fertile, generally poorly drained soils containing an abundance of earthworms for feeding.

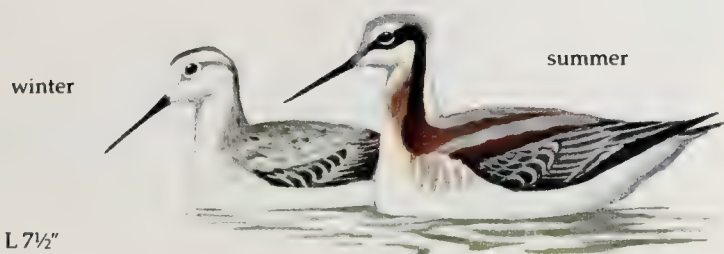
NEST: Nests in a slight depression on dry ground, usually within a few yards of a brushy edge. Also nests on a hummock in wet areas, in open fields, or in young to middle-aged hardwoods of low to medium density.

FOOD: Feeds in open pastures, cultivated fields, and along stream banks, probing in soft mud and leaf litter for earthworms, which make up 50 to 90 percent of the diet. Also eats insect larvae and adults, crustaceans, spiders, seeds, and berries.

REFERENCES: DeGraff et al. 1980, Gregg and Hale 1977, Mendall and Aldous 1943, Owen 1977, Palmer 1967, Sepik et al. 1981, Sperry 1940.

Wilson's Phalarope

Phalaropus tricolor



RANGE: Breeds from southern Yukon and northern Alberta to southern Michigan and southwestern Quebec south to south-central California, east-central Arizona, west-central New Mexico, northern Texas, eastern South Dakota, northern Illinois, northern Indiana, and northern Ohio; isolated breeding in Massachusetts. Winters primarily in South America, casually as far north as southern California and southern Texas.

STATUS: Uncommon.

HABITAT: Once inhabited natural prairies but now found mainly on highly disturbed mixed-grass prairies dotted with small glacial potholes. Also found in taiga broken by moist, grassy muskeg and many small lakes and pools, and in farming country of aspen-grove parklands. Inhabits rolling uplands as high as 6,900 feet in elevation. Outside the breeding season, mainly found on inland wetlands but sometimes on saline or alkaline depressions.

SPECIAL HABITAT REQUIREMENTS: Shallow water bordered by low grasses or sedges.

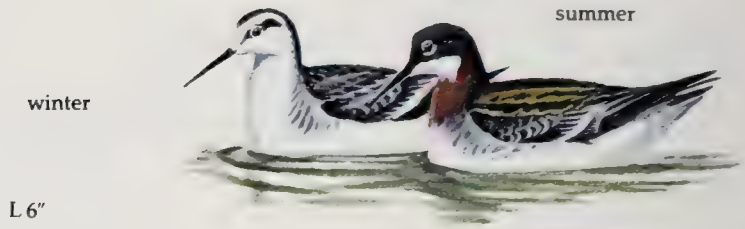
NEST: Nests semi-colonially in a scrapes on the ground around damp meadows with marsh grasses and sedges or rushes. Also nests by shallow sloughs, morasses fringed with short grasses or sedges, lake shores, and in hay meadows or pastures, often 50 to 100 yards from water.

FOOD: Forages on muddy shores and in shallow water; stirs up food by whirling its body around in water. Consumes larvae of mosquitoes and craneflies; predaceous diving beetles, aquatic bugs, brine shrimp, amphipods, eggs of water fleas; and seeds of aquatic plants.

REFERENCES: Bent 1927, Cramp and Simmons 1983, Hohn 1967, Low and Mansell 1983, Palmer 1967.

Red-necked Phalarope

Phalaropus lobatus



RANGE: Breeds from northern Alaska and southern Victoria Island to central Keewatin and southern Baffin Island, south to northwestern British Columbia and northern Alberta across to northern Quebec, and locally along coast of Labrador. Winters mainly at sea in the Southern Hemisphere, largely in tropical and subtropical oceans.

STATUS: Uncommon.

HABITAT: Inhabits the wetter portions of flat alluvial plains, sedge-grass marshlands, clearings in alder and willow scrub, and heath covered slopes above alder and willow scrub. In winter, occurs near upwellings or where other local conditions produce a high biomass of accessible food organisms.

SPECIAL HABITAT REQUIREMENTS: Wet grassy or sedgy terrain interspersed with pools, boreal clearings, or tundra.

NEST: Nests in a small hollow in moss or among sedges, usually atop a small hummock surrounded by water or near a marshy pond or small stream.

FOOD: Forages while swimming, wading, and walking, chiefly on invertebrates. During the breeding season and in migration, eats predominately small insects, especially adult flies and larvae. Also consumes mollusks, crustaceans, spiders, mites, worms, and rarely small fishes and tadpoles, as well as some seeds and algae.

REFERENCES: Bent 1927, Clapp et al. 1983, Cramp and Simmons 1983, Hohn 1968, Palmer 1967.

Franklin's Gull

Larus pipixcan



L11"

RANGE: Breeds from eastern Alberta and central Saskatchewan to western Minnesota, south locally to east-central Oregon, northwestern Wyoming, and northwestern Iowa. Winters primarily in South America, rarely in southern coastal California, and casually along the Gulf Coast of Texas and Louisiana.

STATUS: Common.

HABITAT: Breeds exclusively in shallow freshwater marshes and sloughs in the temperate prairie belt. Favors shallow wetlands up to 6 inches deep with bulrushes, cattails, whitetop, and common reeds, preferably near cultivated lands. In migration and in winter, inhabits sandy beaches, sandbars, fields, and pastures.

SPECIAL HABITAT REQUIREMENTS: Marshes and sloughs with sparse emergent vegetation no denser than one plant less than 3 feet tall per square foot.

NEST: Nests in colonies from a few hundred up to 50,000 pairs. Builds nests on masses of marsh vegetation, often floating on water and anchored to surrounding vegetation. Nests usually near open water.

FOOD: During the breeding season, forages in marshes and fields up to 30 miles from the nesting site. Feeds on a wide variety of foods, especially insects, also taking some amphibians; seeds of wheat, oats, and barley; a few small mammals; and in winter, fish and crustaceans.

REFERENCES: Clapp et al. 1983, Cramp and Simmons 1983, Guay 1968, Low and Mansell 1983, McAtee and Beal 1912.

Bonaparte's Gull

Larus philadelphia



L11"

RANGE: Breeds from western and central Alaska and central Yukon to northern Manitoba, south to southern British Columbia, central Saskatchewan, southern Manitoba, and southern James Bay. Occurs in summer (nonbreeding birds) south to coastal areas in California and New England, and in interior to the Great Lakes. Winters from Washington south along the Pacific Coast into Mexico and from the Great Lakes south through the Ohio and Mississippi Valleys to the Gulf Coast.

STATUS: Common.

HABITAT: Inhabits coastal and interior lowlands, primarily black fly-infested muskeg swamps in taiga up to treeline. Outside the breeding season it occurs on freshwater lakes, rivers, and sloughs, wet meadows, flooded fields, estuaries, shallow coastal waters, bays, and inlets.

SPECIAL HABITAT REQUIREMENTS: Ponds or lakes in swampy muskeg flanked by short to medium conifers.

NEST: Nests in dispersed colonies or noncolonially, from 4 to 20 feet above ground in branches or stumps of spruce, fir, and tamarack, and near water. May also nest in reeds, on mudflats of temporary potholes, and in clumps of bulrushes.

FOOD: Forages in a variety of habitats associated with water, such as marshy ponds, freshwater marshes, rivers, lakes, estuaries, salt marshes, beaches, bays, and open ocean. Eats small fishes, insects, spiders, snails, crustaceans, and marine worms.

REFERENCES: Bent 1921, Clapp et al. 1983, Cramp and Simmons 1983.

Ring-billed Gull

Larus delawarensis

L16"



RANGE: Breeds in the West from southern interior British Columbia and northeastern Alberta to north-central Manitoba south to northeastern California, south-central Colorado and northeastern South Dakota; in the East from north-central Ontario to southern Labrador south to eastern Wisconsin and northern Illinois across to central New Hampshire and New Brunswick. Winters along the Pacific Coast from southern British Columbia south to Mexico; in the interior from the Great Lakes to Mexico and the Gulf Coast; and along the Atlantic Coast from the Gulf of St. Lawrence to the Greater Antilles.

STATUS: Common.

HABITAT: From boreal regions to temperate prairies, inhabits small to moderately sized rocky islands and occasionally peninsulas in large freshwater lakes, rivers, or ponds (a few colonies are on oceanic islands or coasts). Usually avoids densely settled areas. Outside the breeding season, frequents harbors, refuse dumps, sewage outlets, reservoirs, lakes, ponds, streams, coastal bays, estuaries, beaches, and mudflats. Roosts on exposed sandbars and islands.

SPECIAL HABITAT REQUIREMENTS: Islands and peninsulas covered with low vegetation 6 to 54 inches high.

NEST: Frequently nests in mixed colonies with other Laridae, including herring and California gulls. Usually nests on the ground in flat, elevated, sparsely vegetated areas, but sometimes in low trees.

FOOD: Forages in plowed fields, pastures, tidal flats in salt marshes, along the shore, along beaches, and in shallow waters. During the breeding season, feeds extensively on insects, grains, and small fishes. Also eats small rodents, earthworms, and refuse.

REFERENCES: Clapp et al. 1983, Cramp and Simmons 1983, Jarvis and Southern 1976, Vermeer 1970.

California Gull

Larus californicus



L17"

RANGE: Breeds from southern Mackenzie south to northern Utah and north-central Colorado, and west to southern interior British Columbia and northeastern California. Winters from southern Washington and eastern Idaho south, mostly along the Pacific Coast to Mexico.

STATUS: Common.

HABITAT: Inhabits barren islands on fresh, brackish, or alkaline lakes, shores of lakes or ponds, and marshes. Favors sites with low, sparse vegetation. Outside the breeding season it occurs on seacoasts, bays, estuaries, mudflats, irrigated fields, and other agricultural lands.

SPECIAL HABITAT REQUIREMENTS: Open sandy or gravelly lakeshores or islands.

NEST: A colonial nester, often nesting in mixed colonies with the ring-billed gull. Avoids dense herbaceous cover, and constructs its nest in a scrape on the ground in elevated, boulder-strewn areas.

FOOD: Forages opportunistically on shortgrass plains and cultivated lands for a wide variety of foods, including insects, carrion and garbage, earthworms, young birds, bird eggs, and rodents.

REFERENCES: Greenhalgh 1952, Johnsgard 1979, Vermeer 1970.

Herring Gull

Larus argentatus

L20"



RANGE: Breeds from northern Alaska and northern Yukon to central Keewatin, western Baffin Island, and northern Labrador south to south-central British Columbia, central Alberta, northern Minnesota, northeastern Illinois, northern Ohio, northern New York, and along the Atlantic Coast to northeastern South Carolina. Winters from southern Alaska, the Great Lakes region, and Newfoundland south, mostly at sea and along coasts, large rivers and lakes, to Panama.

STATUS: Abundant.

HABITAT: Uses a wide variety of habitats, including sandy, rocky, or wooded islands, stabilized sand dunes, margins of tundra lakes, *Spartina* marshes, cliffs, grass meadows, and buildings. In winter, occurs primarily along the shore of the ocean or other bodies of water, concentrating on beaches and in areas where food is likely to be abundant.

SPECIAL HABITAT REQUIREMENTS: Nesting sites must be free of terrestrial predators and within 25 miles of a dependable source of food.

NEST: Usually nests in exposed sites on the ground in small to large colonies, but occasionally in trees. Prefers to nest in low sites; depending on habitat may nest at the base of boulders, stumps, or bushes on grassy slopes, near large, tall clumps of vegetation, on drift adjacent to salt marshes, or on rock or grassy substrates.

FOOD: Feeds opportunistically in garbage dumps, around seafood-processing operations, in pastures and cultivated fields, on lawns, tundra, and beaches, and at sea. Consumes largely animal matter, including small mammals, birds and bird eggs, amphibians, fishes, shellfishes, and a great variety of invertebrates, plus berries and some fruit, as well as carrion and, at times, garbage.

REFERENCES: Burger and Shisler 1978, Clapp et al. 1983, Cramp and Simmons 1983, Forbush and May 1955.

Caspian Tern

Sterna caspia

L20"



RANGE: Breeds locally in the West from coastal and eastern Washington, eastern Oregon, northern Utah and northwestern Wyoming south to southern California and western Nevada; in the interior from southern Mackenzie to southern James Bay south to North Dakota, northeastern Illinois, and southern Ontario; at scattered localities along the Atlantic Coast from Newfoundland to South Carolina; and along the Gulf Coast from Texas east to Florida. Nonbreeding birds often summer in the James Bay and Great Lakes region, and along both coasts of the United States. Winters primarily in coastal areas from California and North Carolina south to Mexico.

STATUS: Common.

HABITAT: Usually found near the coastline on sandy, stony, or shell beaches, barrier or spoil islands, islands with sand-gravel substrate with little or no vegetation, or on a shell berm in a salt marsh. Tends to occupy less-developed and less-polluted segments of the coast, but is also found inland along shorelines of large lakes. Wintering terns generally are found along beaches, and on isolated spits, often roosting with other larids. In migration, occurs along water courses or in large marshes.

SPECIAL HABITAT REQUIREMENTS: Sparsely vegetated islets or shorelines.

NEST: Usually found in compact colonies, but occasionally nests singly in the vicinity of other tern species in shallow depressions in the ground on bare sandy or rocky soil.

FOOD: Feeds almost entirely on fish 3 to 10 inches long, foraging on species and sizes that are most readily available; also takes crayfish, insects, nestlings and eggs of other birds, and rarely, carrion.

REFERENCES: Clapp et al. 1983, Johnsgard 1979, Ludwig 1965.

Common Tern

Sterna hirundo



L14"

RANGE: Breeds from south-central Mackenzie to southern Quebec and southern Labrador south to eastern Washington and southeastern Alberta, across to central Minnesota, northern Ohio, and northwestern Vermont, and locally along the Atlantic Coast to North Carolina; locally on the Gulf Coast in Texas, Mississippi, and western Florida. Winters in South America, rarely along the coasts of southern California, South Carolina, Florida, and the Gulf Coast.

STATUS: Common; of special concern on the blue list; declining on East Coast.

HABITAT: Uses a variety of habitats, mainly near water, often on islets, and usually in areas with little or no vegetation. Inhabits sparsely vegetated sandy islands, barrier beaches, marshy islands, small islands in salt marshes, or low, small, rocky islands in lakes and rivers. After nesting, typically found along shorelines, on exposed rocks and old pilings, and inshore over shallow coastal waters.

SPECIAL HABITAT REQUIREMENTS: Nesting areas with scant vegetation, isolated from disturbance and predation, and in close proximity to a source of food.

NEST: Builds nests in colonies; nests may vary from a slight hollow in sand or among pebbles to a well-built hollowed mound of grasses and seaweeds, may be in the open or near weeds, grasses, or bushes. Generally prefers sparse cover around the nest.

FOOD: Forages in shallow waters, margins of lakes, or along the coast, but tends to avoid muddy waters. Consumes a diet that varies with locality, including fish less than 6 inches, shrimp and other crustaceans, aquatic worms, insects, and some waste material.

REFERENCES: Burger and Lesser 1978, Forbush and May 1955, Johnsgard 1979, Palmer 1941, Tate and Tate 1982.

Forster's Tern

Sterna forsteri



L14"

RANGE: Breeds from southeastern British Columbia and central Alberta to central Manitoba, south to southern California and south-central Idaho, across to central Kansas, northern Iowa, and northwestern Indiana; along the Atlantic Coast from southern New York south locally to North Carolina; and along the Gulf Coast from Texas east to Louisiana. Winters along the Pacific and Atlantic Coasts from central California and Virginia south to Central America.

STATUS: Common.

HABITAT: Primarily inhabits large saltwater and freshwater marshes; also found on marshy bays, marshy parts of islands, marshy edges of streams and lakes, sloughs, dikes in evaporation ponds, estuarine islands, marshes adjacent to barrier beaches, and dredge-spoil islets. In winter, occurs in harbors, marshy bays, estuaries, lagoons, and inlets along coastal areas, occasionally occurring inland along lakes and ponds.

SPECIAL HABITAT REQUIREMENTS: Extensive marshy areas with vegetated nest sites partly open to water.

NEST: Usually found in small colonies, nesting on mats of floating dead vegetation, flattened reeds and cattails, large muskrat houses near the edges of open pools of water, floating rootstalks of cattails, or sometimes in a shallow depression in sand or mud. May also locate nests on sand or gravel bars, beaches, or grassy islands. Sometimes uses old or abandoned nests of western and pied-billed grebes.

FOOD: Feeds over or near the marshes in which it nests. Eats small fish, insects, crustaceans, and frogs.

REFERENCES: Bergman et al. 1970, Clapp et al. 1983, Forbush and May 1955, Johnsgard 1979, Low and Mansell 1983, McNicholl 1971.

Least Tern

Sterna antillarum



L8½"

RANGE: Breeds along the Pacific Coast from central California south to southern Baja California, inland along the Colorado, Red, Missouri, and Mississippi River systems from southern South Dakota, western Iowa, Southwestern Missouri, northwestern Indiana, central Louisiana, northeastern Texas, central Oklahoma, western Kansas, and central New Mexico, and along the Atlantic Coast from Maine to Florida and west to Texas. Winters along the Pacific Coast from Baja California and along the Gulf Coast to South America.

STATUS: Threatened in the Great Plains; endangered along California Coast; stable along Atlantic Coast, but is listed on New Jersey and Maine's threatened and endangered lists.

HABITAT: Inhabits river sandbars, inland islands, broad areas of sand or gravel beaches, and newly cleared land along the coast. Frequents salt plains in Oklahoma.

SPECIAL HABITAT REQUIREMENTS: Open, sandy coastal beaches, and river sandbars for nesting.

NEST: Nests solitarily or in scattered colonies. Nests in scrapes (with little or no lining) in sand or gravel (gravel or pebble substrates are preferred) above ordinary tides. Shares habitat with piping plover in the Great Plains.

FOOD: Skims the surface of the water or hovers and dives for food, sometimes spears fish with closed bill. Eats sand eels, shrimp, and small fish.

REFERENCES: Bent 1921, Tompkins 1959, Johnsgard 1979, Terres 1980.

Black Tern

Chlidonias niger



L9"

RANGE: Breeds from southwestern and east-central British Columbia and south-central Mackenzie to southern Quebec and southern New Brunswick, south locally to south-central California and northern Utah, across to Nebraska, south-central Illinois, Pennsylvania, and Maine. Nonbreeding birds occur in summer south on the Pacific Coast to Panama, and in eastern North America to the Gulf Coast. Winters in South America.

STATUS: Common; overall population is stable or decreasing slightly.

HABITAT: Found in taiga and on the plains and prairies, where it inhabits shallow marshes, open areas of deeper marshes, reed-bordered sloughs, natural ponds, lakes, fish and stock ponds, shallow river impoundments, wet meadows, river oxbows, ditches, edges of streams, and swampy grasslands. In migration, frequents freshwater and saltwater, occurring along the coast and along marshes, rivers, lakes and nearby cultivated fields.

SPECIAL HABITAT REQUIREMENTS: Aquatic habitats with extensive stands of emergent vegetation and large areas of open water.

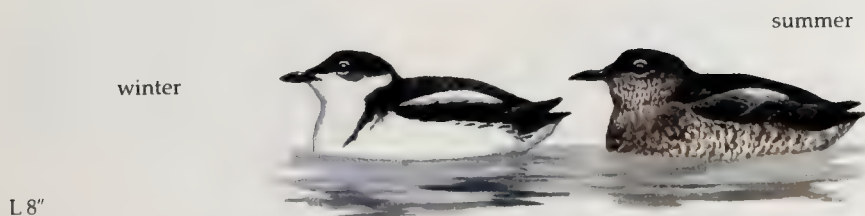
NEST: Often nests in small colonies, but occasionally nests singly. Usually places nest on a floating mass of vegetation such as cattails and bulrushes and anchored to surrounding vegetation, on floating pieces of wood, or in a slight hollow atop a muskrat house. Prefers areas of emergent vegetation over water up to 3 feet deep or near open water. Sometimes uses abandoned nests of other birds including grebes, Forster's terns, and American coots.

FOOD: Does not compete strongly with fish-eating species; consumes a diet that includes aquatic and land insects, worms, small mollusks, crustaceans, and a few small fishes and grubs.

REFERENCES: Clapp et al. 1983, Forbush and May 1955, Johnsgard 1979, Low and Mansell 1983, McNicholl 1971, Tate and Tate 1982.

Marbled Murrelet

Brachyramphus marmoratus



RANGE: Breeds from Alaska south to central California. Winters, off shore, from southern Alaska to central California (casually to southern California).

STATUS: Locally common.

HABITAT: Inhabits coniferous forests, coastal islands, and inland lakes, usually within 12 miles from ocean.

SPECIAL HABITAT REQUIREMENTS: Old growth coniferous forests.

NEST: Nests solitarily on bare rocks, below ledges, in rock cavities, on the ground, and in coniferous trees. Usually nests within 4 miles of the ocean but occasionally farther inland.

FOOD: Dives for food and consumes mostly small fish and various crustaceans but diet varies regionally.

REFERENCES: Terres 1980, Day et al. 1983, Carter and Sealy 1986.

Rock Dove

Columba livia



L11"

RANGE: Resident from southern Alaska and southern Canada south throughout North America. Introduced; originally an Eurasian species.

STATUS: Common.

HABITAT: May inhabit narrow, steep-walled canyons and rocky cliffs, but far more commonly found near human habitations.

NEST: Prefers to nest on or in structures that provide narrow ledges similar to cliff ledges. Constructs a flimsy nest on stone, brick, and concrete buildings in cities, high upon ledges, under windows, under bridges, on monuments, in barns or other man-made structures, preferably in semi-dark cavities. May nest singly or in colonies.

FOOD: Commonly feeds on parkland, sidewalks, and parking lots in cities; cultivated fields; feedlots; and wastelands. Gleans seeds of weeds, grasses, and grains, takes human handouts, and eats a few berries and tender roots of grasses.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Terres 1980.

White-crowned Pigeon

Columba leucocephala

L11"



RANGE: Breeds in southern Florida on islets in the Florida Keys, throughout Florida Bay, the Lesser Antilles, and islets of Central America. Nonbreeding birds may occur in summer in southern peninsular Florida. Winters from southern peninsular Florida and the Florida Keys throughout most of the breeding range to central America.

STATUS: Common.

HABITAT: Generally gregarious; breeds and roosts in large concentrations on brushy, small, low islands and keys, among coastal mangroves and pines.

NEST: Nests colonially, but not with or near other colonial species. Builds nest from a few feet to 15 feet or more above ground, on top of cactus or bushes, or high in mangroves; occasionally low and over water.

FOOD: Forages in open forests, woodlands, and scrubs and eats seeds, berries, and a few insects.

REFERENCES: Cottam and Knappen 1939, Harrison 1975, Sykes in Farrand 1983b, Terres 1980, Wiley and Wiley 1979.

Red-billed Pigeon

Columba flavirostris



L11"

RANGE: Breeds in the lower and middle Rio Grande Valley in southern Texas south through Mexico into Central America; mostly absent in winter.

STATUS: Local and uncommon.

HABITAT: Inhabits semiarid woodlands near water. In Texas, it is found in river thickets containing tall timber and a thick undergrowth of thorny shrubs including ebony blackbead, huisache, mesquite, baldcypress, great leucaena, Mexican ash, elm, black willow, and hackberry. Often perches on exposed bare branches high in trees.

SPECIAL HABITAT REQUIREMENTS: Tall dense brush with small patches of tall trees.

NEST: Nests 8 to 30 feet above ground on a horizontal tree branch, in a clump of small branches, or in a tree concealed by a tangle of vines or brush.

FOOD: Forages high in the crowns of trees and in stubble fields on a diet that includes fruits of hackberries, condalia, and wild grape; acorns; and waste grains.

REFERENCES: Bent 1932, Oberholser 1974a, Terres 1980.

Band-tailed Pigeon

Columba fasciata



L13"

RANGE: Breeds from southeastern Alaska and southwestern British Columbia south through the mountains of Washington, Oregon, California, and extreme western Nevada to Baja California; and from southern Nevada, Arizona, central Utah, north-central Colorado, New Mexico, and western Texas south to Honduras. Winters from central California, central Arizona, and western Texas south to Honduras.

STATUS: Locally common.

HABITAT: Along the Pacific Coast, inhabits a variety of forest lands with western hemlock, western redcedar, and Douglas-fir to ponderosa pine, white fir, or incense cedar. In Oregon and Washington, prefers forest land with a good interspersed of seral stages and openings; in California, prefers forests, woodlands, or chaparral with an abundance of oak. In the interior, occupies habitats ranging from montane oak woodlands to arid woodlands of pinyon pine and oaks, and from agricultural areas near forests to berry-producing areas at 11,000 feet elevation. Occasionally found in spruce-fir associations characterized by Engelmann spruce, subalpine fir, lodgepole pine, limber pine, and aspen, but prefers sites dominated by ponderosa pine and Gambel oak.

SPECIAL HABITAT REQUIREMENTS: Mature conifers or broad leaved trees at least 8 feet tall for nesting and a source of mineral water or salt deposits in early fall and winter.

NEST: Nests in coniferous or deciduous trees usually located near a clearing and on a moderate to steep slope or precipice. Conceals nest on horizontal branches typically 15 to 40 feet high, rarely on the ground.

FOOD: Gleans sometimes exclusively on one species or source of food as long as the supply lasts. Mainly eats mast and berries, but also eats acorns, pine nuts, pinyon nuts, blossoms, green and ripe fruits, and some waste grains.

REFERENCES: Jeffrey 1977, Johnsgard 1975a, Neff 1947, Peeters 1962.

White-winged Dove

Zenaida asiatica



L10"

RANGE: Breeds from southeastern California and southern Nevada to southwestern Texas south, through Central America into western South America. Introduced and established in southern Florida. Winters generally in the breeding range, but northern birds are mostly migratory, casually ranging north to northern California and Colorado and occurring regularly along the Gulf Coast east to Florida.

STATUS: Locally abundant.

HABITAT: Occupies a variety of habitats in semiarid woodlands. Prefers tall, dense, or brushy riparian woodlands, with trees from 15 to 25 feet tall and an understory of thorny shrubs. Also occupies desert scrub, desert grassland, oak woodland, chaparral, valleys of desert mountains, and shade and fruit trees of agricultural areas, country roadsides, and suburban residential areas.

SPECIAL HABITAT REQUIREMENTS: Nest sites with trees of low to medium height having dense foliage and fairly open ground cover.

NEST: Builds nests on relatively horizontal branches of a variety of trees and large shrubs in shaded sites, preferably in the interior of woodlands and thickets.

FOOD: Forages in shelter of thickets, weeds, or fields for seeds. Also eats mast, fruit, and some insects.

REFERENCES: Brown 1977, Cottam and Trefethen 1968, Neff 1940, Oberholser 1974a.

Mourning Dove

Zenaida macroura



L10"

RANGE: Breeds from southern and central Alberta to southern New Brunswick and Nova Scotia south to Mexico. Winters primarily from northern California east across the central United States to Iowa, southern Michigan, southern Ontario, New York, and New England south throughout the breeding range to central Panama.

STATUS: Abundant.

HABITAT: Occupies a broad range of habitats from desert areas close to water to a variety of wooded habitats, but avoids densely forested regions. Inhabits open country, especially fields, orchards, or generally weedy areas having an abundance of grains and seeds. Also inhabits open mixed woodlands and wood edges, shelterbelts, church and cemetery sites, evergreen plantations, suburbs, and cities.

SPECIAL HABITAT REQUIREMENTS: Open country with some bare ground and adequate foods.

NEST: Loosely colonial or solitary. Generally nests on horizontal branches in shrubs and trees, especially conifers up to 100 feet, but typically 10 to 25 feet above ground, and occasionally on the ground.

FOOD: Feeds primarily on weed seeds and waste grains. Also eats a few insects, small snails, fruits, and nuts.

REFERENCES: Davison and Sullivan 1963, DeGraff et al. 1980, Forbush and May 1955, Hanson and Kosack 1963, Johnsgard 1975a, Keeler 1977.

Inca Dove

Columbina inca



L6½"

RANGE: Resident from extreme southeastern California, central Arizona, southern New Mexico, and central Texas south to Costa Rica.

STATUS: Common to abundant.

HABITAT: Primarily found in the vicinity of human habitations, especially around introduced broad-leaved deciduous trees, exotic conifers, and native live oaks in areas with little or no understory. Inhabits poultry and livestock feedlots, yards, gardens, orchards, school grounds, city parks, and roads through brushy mesquite pastures, usually near a source of water. Roosts in evergreen trees.

NEST: Nests on a horizontal fork or flattened tree limb or in a bush, 4 to 25 feet above ground in a brushy pasture, or more often in the immediate vicinity of houses. Builds nests in native shrubs (including catclaw and chollas), in baldcypress, in shade trees, on top of utility poles, in hanging baskets near a house, and sometimes in nests of other species including mourning doves, mockingbirds, and cactus wrens. Generally uses nests for 2 or more consecutive nestings.

FOOD: Feeds almost entirely on the ground, taking seeds of a wide variety of native plants. Eats wheat, cracked corn, oats, and milo readily if available.

REFERENCES: Anderson and Anderson 1948, Harrison 1979, Johnston 1960, Oberholser 1974a.

Common Ground-Dove

Columbina passerina
(formerly Ground Dove)



L5½"

RANGE: Resident from southern California, central Arizona, southern New Mexico, central Texas, the Gulf Coast, and South Carolina south to South America.

STATUS: Common, locally abundant.

HABITAT: Inhabits sparsely wooded areas with low undergrowth, roadsides, fields, orchards, sandy reefs, and open sandy areas in forest and savannah; over much of its range, is now primarily around farms and towns. In Texas, occurs in grassy mesquite-live oak-cactus savannah and to some extent scrubby juniper-oak areas; in Georgia and South Carolina, occurs mainly near beaches and sea islands with tall beach grass. In Arizona, inhabits river bottomlands with mesquite or tamarisk woods.

SPECIAL HABITAT REQUIREMENTS: Open areas with plants that produce small seeds.

NEST: Uses a wide range of sites for nesting. May nest in a slight hollow on the ground, in a low bush, or in a tree, up to 25 feet above the ground.

FOOD: Feeds primarily on small seeds gathered from gardens and lawns, along roadsides, in fields, weed patches, or grassy areas. Also takes a few berries and some insects.

REFERENCES: Bent 1932, Forbush and May 1955, Goodwin 1967, Oberholser 1974a, Phillips et al. 1964.

Black-billed Cuckoo

Coccyzus erythrophthalmus



L 11"

RANGE: Breeds from east-central and southeastern Alberta and southern Saskatchewan to New Brunswick and Nova Scotia south, at least locally, to eastern Colorado, north-central Texas, northern Arkansas, northern Alabama, and the Carolinas. Winters in South America.

STATUS: Common.

HABITAT: Prefers extensive areas of upland woods that provide a variety of trees, bushes, and vines. Also occurs in brushy pastures, hedgerows, open woodlands, orchards, thickets, and along wooded roadsides.

SPECIAL HABITAT REQUIREMENTS: Low, dense, shrubby vegetation.

NEST: Selects nest sites that are well concealed by overhanging branches and leaf clusters. Usually nests in shrubs or on a low tree branch, typically 4 to 6 feet above ground. Occasionally lays eggs in the nests of other birds.

FOOD: Feeds primarily on caterpillars, especially tent caterpillars; also other insects, spiders, and a few tiny mollusks, fishes, and wild fruits and berries.

REFERENCES: Beal 1904, Bent 1940a, DeGraff et al. 1980, Herrick 1910, Johnsgard 1979, Spencer 1943.

Yellow-billed Cuckoo

Coccyzus americanus



L 11"

RANGE: Breeds from interior California and northern Utah to southwestern Quebec and southern New Brunswick, south to southern Arizona and into Mexico. Winters in South America.

STATUS: Common.

HABITAT: Favors moderately dense thickets near watercourses, second-growth woodlands; deserted farmlands overgrown with shrubs and brush, and brushy orchards for habitat. Also inhabits open woods, avoiding extremely dense woods and high elevations.

SPECIAL HABITAT REQUIREMENTS: Low, dense, shrubby vegetation.

NEST: Prefers to nest in thick bushes overgrown with vines or in trees on horizontal limbs, typically 4 to 8 feet above ground. Conceals nest with surrounding foliage.

FOOD: Forages among leaves for food, which consists mainly of caterpillars, especially tent caterpillars and fall webworms. Also eats other insects and spiders, some small wild fruits, some frogs, and occasionally a small lizard.

REFERENCES: Beal 1904, Bent 1940a, DeGraff et al. 1980, Johnsgard 1979, Preble 1957, Tate and Tate 1982.

Mangrove Cuckoo

Coccyzus minor



RANGE: Breeds in southern Florida from Tampa Bay and Miami southward in coastal areas, including the Florida Keys through Mexico to South America. Winters throughout the breeding range, but mostly south of Florida.

STATUS: Rare and local.

HABITAT: Inhabits red and black mangrove thickets and swamps near saltwater, and upland hardwood hummocks.

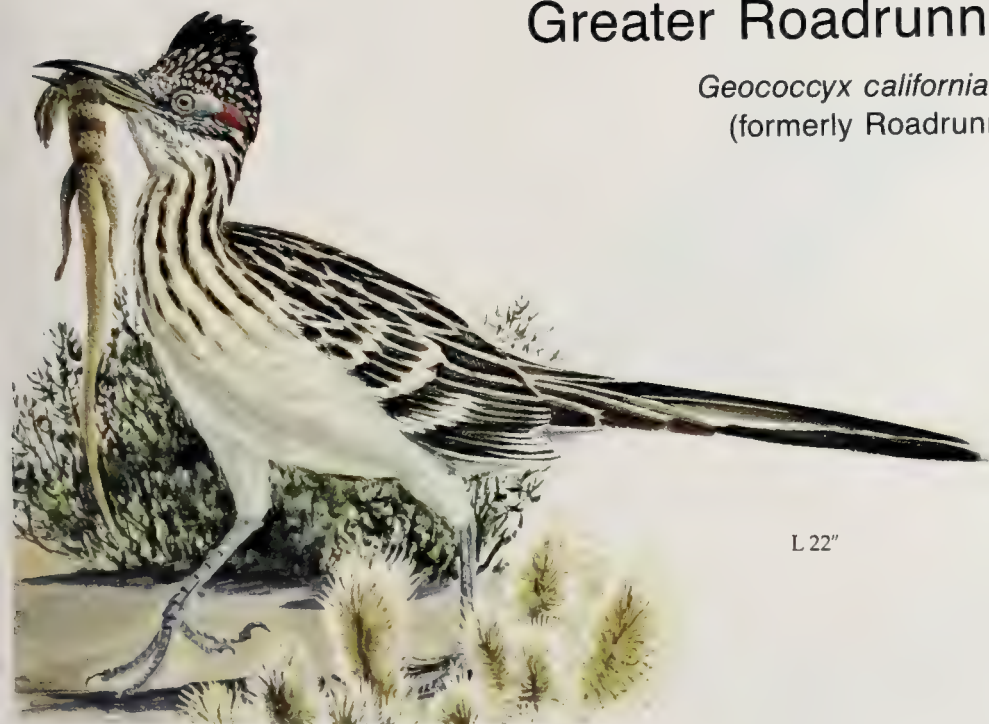
NEST: Typically builds nest on a horizontal mangrove branch, that is indistinguishable from the nest of the yellow-billed cuckoo.

FOOD: Often feeds in open fields and clearings near thickets on caterpillars and other insects, spiders, and a few small fruits and wild berries.

REFERENCES: Bent 1940a, Harrison 1975, Sykes in Farrand 1983b, Terres 1980.

Greater Roadrunner

Geococcyx californianus
(formerly Roadrunner)



L 22"

RANGE: Resident from northern California (rarely) and western and central Nevada east to southern Kansas and north-central Louisiana south to Mexico.

STATUS: Common.

HABITAT: Typically associated with desert regions, but also found in chaparral, grasslands, open woodlands of pine and oak, agricultural areas, and moist woodlands. Frequents edge habitats provided by a mixture of open land, brush, and forest; also at home among tall pines and magnolias or mesquite and cactus.

SPECIAL HABITAT REQUIREMENTS: Bare areas with some scattered trees and bushes.

NEST: Usually nests in a low tree, bush, thicket, or clump of cactus from 3 to 15 feet above ground, rarely on the ground. In desert regions, builds nest so that bands of shade cross the nest during the extreme heat of the day; prefers staghorn cholla for nesting site in arid regions.

FOOD: Feeds primarily on animals, with about 10 percent of the diet consisting of vegetable matter. Eats a great variety of insects, spiders, scorpions, snails, lizards, and small snakes; also eats some young birds and small mammals, and fruits and seeds.

REFERENCES: Bryant 1916, Johnsgard 1979, Oberholser 1974a, Ohmart 1973, Terrill in Farrand 1983b.

Smooth-billed Ani

Crotophaga ani



L 12"

RANGE: Resident in central and southern Florida from Tampa Bay and Merritt Island region southward, especially from Lake Okeechobee area to Dade County into Central and South America.

STATUS: Locally common.

HABITAT: Inhabits dense brush or hedgerows near fields, pastures, and marshes, roadside thickets, gardens and thick woods in cities, towns, and around farms.

NEST: May nest singly or communally, with several females laying their eggs in a single nest. The nest is constructed in trees or dense shrubs 6 to 30 feet above ground, commonly near human habitation.

FOOD: Forages in moist open meadows for grasshoppers, crickets, moths, green tree frogs, and chameleons.

REFERENCES: Harrison 1975, Kaufman in Farrand 1983b, Merritt 1951.

Groove-billed Ani

Crotophaga sulcirostris



L 14"

RANGE: Resident in central and southern Texas and southern Louisiana south through Mexico and Central America to South America.

STATUS: Common to uncommon.

HABITAT: Tolerant of a wide range of ecological conditions, inhabiting brushy pastures, orchards, light second growth, lawns and clearings near homes, marshes, and moist thickets along rivers. Also found in semi-desert areas with scattered cacti and acacias and thickets of ebony blackbead, mesquite, and Jerusalem-thorn. Frequently accompanies livestock, which stir insects from the grass.

SPECIAL HABITAT REQUIREMENTS: Open areas with low vegetation for foraging, and trees and bushes for roosting and nesting.

NEST: Builds nest from 2 to 25 feet up in densely foliated trees or, in arid regions, in opuntias and other cacti. May nest singly or communally, with several females laying their eggs in a single nest.

FOOD: Forages in pastures and farm fields, feeding on insects stirred up by cattle. Eats mainly insects, including grasshoppers, termites, and roaches, plus spiders, small lizards, and berries.

REFERENCES: Kaufman in Farrand 1983b, Oberholser 1974a, Skutch 1959, Terres 1980.

Common Barn-Owl

Tyto alba
(formerly Barn Owl)



L14"

RANGE: Resident from southwestern British Columbia, southern Idaho, and Montana east to southern Vermont and Massachusetts south through the United States to South America. Northernmost populations are partially migratory, wintering south to southern Mexico and the West Indies.

STATUS: Uncommon; overall population level is low, but stable.

HABITAT: Found in open to semiopen habitats such as prairie, farmland, savannah, marshland, and desert, but prefers the vicinity of farms and towns. Avoids woodlands and higher elevations.

SPECIAL HABITAT REQUIREMENTS: Abundant supply of small mammals for food, and hollow trees, old buildings, barns, cavities, or caves for nesting and roosting.

NEST: Nests in a variety of sites. Favors natural tree hollows, especially in live oaks near a marshy meadow. Typically nests in old barns, church and school steeples, silos, or abandoned buildings. Also uses protected ledges along cliff faces, abandoned underground burrows of badgers, woodchucks, or other mammals, caves, cavities in high stream banks (8 to 10 feet above water level), abandoned nests of crows, hawks, or magpies, and artificial nest sites. Will return to the same nest site year after year if undisturbed.

FOOD: Hunts by night over marshes, meadows, fields, barnyards, brushy areas, pastures, and other open areas for small mammals, especially mice, and occasionally small birds and large insects. Also eats some frogs, snakes, lizards, and crayfish.

REFERENCES: Coats in Farrand 1983b, DeGraff et al. 1980, Hawbecker 1945, Heintzelman 1979, Johnsgard 1979, Karalus and Eckert 1974, Tate and Tate 1982.

Flammulated Owl

Otus flammeolus



L6"

RANGE: Breeds locally from southern British Columbia, southern Idaho, and northern Colorado south to southern California, southern Arizona, southern New Mexico, western Texas and Mexico. Winters in Mexico, casually north to southern California.

STATUS: Rare to locally common.

HABITAT: Inhabits forests of the western mountains, mostly from 4,500 to 7,800 feet but as high as 10,000 feet elevation. Prefers woods with dense, thicketlike cover close to relatively open areas. Favors ponderosa pine forests but also occurs in forests of spruce-fir, Douglas-fir, lodgepole pine, aspen, and pinyon-juniper.

SPECIAL HABITAT REQUIREMENTS: Some undergrowth or intermixture of oaks in the forest.

NEST: Usually nests in abandoned flicker or other woodpecker nest cavities from 7 to 25 feet above ground in aspen, oaks, or pines. Will forceably evict a flicker if an abandoned cavity is not available; rarely nests in holes constructed by bank swallows.

FOOD: Consumes a diet of insects and other invertebrates such as spiders, scorpions, and centipedes; prefers moths, beetles, crickets, and grasshoppers and will sometimes eat small birds and small mammals.

REFERENCES: Coats in Farrand 1983b, Heintzelman 1979, Karalus and Eckert 1974, Oberholser 1974a, Phillips et al. 1964.

Eastern Screech-Owl

Otus asio

Western Screech-Owl

Otus kennicottii
(formerly Screech Owl)



gray phase

L8"

red phase



RANGE: Eastern Screech-Owl; Resident from southern Manitoba and northern Minnesota to southwestern Quebec and Maine, south through the eastern United States, eastern Montana, eastern Colorado, and western Oklahoma to southern Texas, and across to southern Florida. Western Screech-Owl; Resident from south-coastal and southeastern Alaska, coastal and southern British Columbia, and northern Idaho to southeastern Colorado and extreme western Oklahoma, south to Mexico and western Texas.

STATUS: Common; populations are declining in the West, but are stable in the East.

HABITAT: Found in a variety of habitats, favors oak and riparian woodlands in the West, and open woodlands adjacent to meadows, marshes, or fields in the East. Also inhabits orchards, shade trees in towns and cities, small woodlots, and deciduous forests. Prefers areas with widely spaced trees interspersed with grassy open spaces for hunting.

SPECIAL HABITAT REQUIREMENTS: Cavities for nesting and roosting in trees with a minimum dbh of 12 inches.

NEST: Nests in natural cavities in trees or in old woodpecker holes, especially those of the northern flicker and pileated woodpecker. Chooses cavities with openings 3 to 5 inches in diameter that are typically 5 to 30 feet (but up to 50 feet) above the ground. Many use same cavity for many years; will use artificial cavities.

FOOD: Hunts for its food in grassy openings, fields, meadows, or along wooded field margins or streams. Primarily takes rodents, especially meadow voles, but also eats insects, scorpions, spiders, centipedes, crayfish, amphibians, reptiles, fishes, and small birds.

REFERENCES: DeGraff et al. 1980, Earhart and Johnson 1970, Heintzelman 1979, Johnsgard 1979, Karalus and Eckert 1974, Scott et al. 1977, Tate and Tate 1982, Thomas et al. 1979, Van Camp and Henny 1975.

Whiskered Screech-Owl

Otus trichopsis
(formerly Whiskered Owl)



L6½"

RANGE: Resident from southeastern Arizona south to Nicaragua.

STATUS: Common.

HABITAT: Inhabits scattered to dense woodlands on the slopes of valleys and in canyons, from 4,000 to 7,000 feet (usually between 5,500 and 6,500) feet in elevation. Occurs in dense oak, oak-pine, and sycamore woodlands, avoiding forests of pure pines or firs.

SPECIAL HABITAT REQUIREMENTS: Cavities in trees for nesting.

NEST: Nests in natural cavities in trees or in abandoned nest cavities of northern flicker and other woodpeckers. Prefers cavities in large branches or stubs to cavities in tree trunks. Favors relatively deep holes with bottoms 14 to 16 inches below the cavity entrance. Usually chooses a nest site that is 10 to 20 feet above the ground, generally in white oaks, but also uses other species.

FOOD: Consumes a diet mostly of insects and other invertebrates, including crickets, large moths, beetles, grasshoppers, large caterpillars, scorpions, centipedes, some small mammals, and rarely, small birds.

REFERENCES: Heintzelman 1979, Karalus and Eckert 1974.

Great Horned Owl

Bubo virginianus



L20"

RANGE: Breeds from western and central Alaska and central Yukon to Labrador and Newfoundland, south throughout the Americas to Tierra del Fuego. Winters generally throughout the breeding range, with the northernmost populations being partially migratory.

STATUS: Common.

HABITAT: Occurs in a wide variety of forested habitats. Inhabits open coniferous, deciduous, or mixed woodlands, orchards, second-growth forests, marshes, swamps, riverine forests, partially wooded slopes, brushy hillsides, farm woodlots, large city parks, and rocky canyons well away from forest cover. In the South, prefers baldcypress hummocks and expansive dense palmetto woodlands interspersed with scattered pine.

SPECIAL HABITAT REQUIREMENTS: Large abandoned bird nests or large cavities for nesting.

NEST: Uses a wide variety of nest sites up to 70 feet aboveground; frequently abandoned nests of hawks, herons, or crows. Also uses large tree cavities, crotches, stumps, caves, and ledges. Occasionally, constructs a nest but most often uses abandoned nests.

FOOD: Prefers open areas near woodlands such as marshes or meadows for hunting. Consumes an extremely varied diet; will attempt to kill animals up to the size of a turkey or porcupine, but prefers small to medium-sized mammals and birds. Also preys upon reptiles, amphibians, large insects, and fishes; rarely consumes carrion.

REFERENCES: DeGraff et al. 1980, Earhart and Johnson 1970, Heintzelman 1979, Johnsgard 1979, Karalus and Eckert 1974, Sprunt 1955.

Snowy Owl

Nyctea scandiaca



L20"

RANGE: Breeds from northern Alaska and northern Yukon to Prince Patrick and northern Ellesmere islands, south to coastal western Alaska, northern Mackenzie and southern Keewatin across to northern Quebec and northern Labrador. Winters irregularly south to southern Canada, Minnesota, and New York, and occasionally further south.

STATUS: Common in the far North, rare and local in the conterminous United States.

HABITAT: Found north of the tree line in arctic tundra, where it inhabits moss- and lichen-covered flatlands, lowlands, and valleys well dotted with frost-heave mounds, hillocks, or rocks. Avoids very marshy areas with no raised sites. During years of low lemming abundance, moves southward into the conterminous United States, onto open fields, sandy beaches, barrier islands, and marshes.

SPECIAL HABITAT REQUIREMENTS: Raised sites such as frost-heave mounds several yards in diameter and as much as 2 to 3 feet above the ground, large rocks, or other abrupt rises in the ground for roosting and nesting.

NEST: Generally nests at elevations less than 650 feet. Nests in a shallow depression on top of a frost-heave mound or other raised site, occasionally on a gravel bank, tidal flat, or on slopes above a marsh or lake. Rarely, nests in an abandoned eagle nest high in a tree.

FOOD: Kills a wide variety of mammals and birds, especially lemmings and mice. Throughout its summer and winter range, also preys on a variety of rodents, rabbits, waterfowl, shorebirds, songbirds, fish—almost any small animal that can be caught.

REFERENCES: Heintzelman 1979, Karalus and Eckert 1974, Udvardy 1977, Watson 1957.

Northern Hawk-Owl

Surnia ulula



RANGE: Breeds from tree-line in western and central Alaska to southern Keewatin, central Labrador south to southern Alaska, northern Minnesota, northern Michigan, and New Brunswick. Winters from the breeding range southward irregularly to southern Canada and northern Minnesota, and casually the northern United States.

HABITAT: Inhabits much of the northern open coniferous or mixed forests, forest edges, clearings, old burns, dense brushy areas (especially tamarack), scrubby second-growth woodlands, and muskeg.

SPECIAL HABITAT REQUIREMENTS: Open woodlands with cavities for nesting.

NEST: Usually nests in natural cavities or in enlarged holes of pileated woodpeckers and flickers, but also in birch, spruce, and poplar snags. Occasionally nests on cliffs or in crow's nests.

FOOD: Hunts extensively during the day, preying on small mammals (especially mice), birds, and insects. In summer, consumes primarily small mammals and insects. Preys on ptarmigan during winter when other foods are scarce.

REFERENCES: Bent 1938, Henderson 1919, 1925, Mendall 1944.

Northern Pygmy-Owl

Glaucidium gnoma
(formerly Pygmy-Owl)



L6"

RANGE: Resident from southeastern Alaska, British Columbia, southwestern Alberta, and western Montana south, mostly in mountainous regions through southern California and interior Mexico to Central America, and extending east as far as central Colorado, central New Mexico, and extreme western Texas.

STATUS: Common.

HABITAT: Inhabits deciduous, coniferous, and mixed forests in the West. In Arizona, prefers mixed oak-pine forests on south-facing slopes from 4,000 to 13,000 feet in elevation, but tends to frequent coniferous forests at the higher elevations; in California, occurs up to 6,000 feet, primarily in mixed scattered hardwoods and conifers. In the Rocky Mountains, occurs from 5,000 to 10,000 feet in dense pine forests or open areas with scattered trees; along the Pacific Coast, prefers dense damp forests of firs, redwoods, and cedars.

SPECIAL HABITAT REQUIREMENTS: Natural cavities or old woodpecker holes for nesting.

NEST: Nests in abandoned cavities of the hairy woodpecker or northern flicker or natural cavities. Chooses cavities from 8 to 100 feet above the ground; in Rocky Mountains uses cavities up to 24 feet above the ground; in California, from 40 to 75 feet, and along the coast from 50 to 60 feet (but up to 100 feet) above the ground. May use the same nest site for several years.

FOOD: Primarily preys upon mice and large insects; also eats other small mammals, small birds, spiders, scorpions, centipedes, small snakes, lizards, and toads.

REFERENCES: Earhart and Johnson 1970, Heintzelman 1979, Karalus and Eckert 1974.

Ferruginous Pygmy-Owl

Glaucidium brasilianum
(formerly Ferruginous Owl)



L6"

RANGE: Resident from south-central Arizona and southern Texas south through Mexico to South America.

STATUS: Rare and local.

HABITAT: Inhabits wooded river bottoms of cottonwoods and mesquite, but prefers densely vegetated desert areas with saguaro and cholla cacti and mesquite thickets. It is found from sea level to 4,000 feet.

SPECIAL HABITAT REQUIREMENTS: Abandoned woodpecker holes for nesting.

NEST: Nests in abandoned woodpecker cavities from 10 to 40 feet above the ground in cottonwoods, mesquite, and most often in saguaro cactus. May use same nest sites year after year.

FOOD: Hunts from a perch, preying primarily on crickets, other large insects, and lizards. Also eats scorpions, caterpillars, and small birds and mammals.

REFERENCES: Heintzelman 1979, Karalus and Eckert 1974, Oberholser 1974a, Terres 1980, Terrill in Farrand 1983b.

Elf Owl

Micrathene whitneyi



L5½"

RANGE: Breeds from southeastern California, extreme southern Nevada, central Arizona, southwestern New Mexico, and western and southern Texas south to Mexico. Winters in Mexico.

STATUS: Common.

HABITAT: Prefers arid, low elevation desert areas overgrown with cacti, mesquite, and creosote bush, or with agave, ocotillo, and cactus desert scrub. Also inhabits riparian cottonwood and willow groves; mesquite floodplains; walnut, sycamore, and oak woodlands; and juniper, pinyon pine, and oak woodlands up to 7,000 feet in elevation. Avoids pure stands of pine, but will inhabit almost every other type of dry, woody vegetation.

SPECIAL HABITAT REQUIREMENTS: Abandoned woodpecker holes for nesting.

NEST: Nests in abandoned woodpecker holes, especially in saguaro cactus but also in agave bloom stalks, tree stumps, cottonwoods, mesquite, sycamore, pines, walnut oaks, or willows growing on mesas and desert slopes and in canyons. Nests generally 10 to 30 feet above the ground.

FOOD: Preys primarily on large insects but also eats scorpions and rarely lizards, snakes, and small birds.

REFERENCES: Heintzelman 1979, Karalus and Eckert 1974, Ligon 1968, Oberholser 1974a.

Burrowing Owl

Athene cunicularia



L8"

RANGE: Breeds from southern interior British Columbia to southern Manitoba south through eastern Washington, central Oregon, and California to Baja California, east to western Minnesota, western Missouri, Oklahoma, eastern Louisiana, and south to Mexico and Central America; also in Florida. Winters throughout breeding range except for the northern portions in the Great Basin and Great Plains regions.

STATUS: Locally common; populations declining due to widespread elimination of burrowing rodents, notably prairie dogs and ground squirrels.

HABITAT: Prefers nonforested plains, grasslands, deserts, and sometimes open areas such as vacant lots near human habitations or airports. Largely depends on mammals that dig burrows in open areas with short vegetation for nesting, roosting, and for escape. Commonly perches on fence posts, bushes, utility wires, roadside billboards, and burrow mounds.

SPECIAL HABITAT REQUIREMENTS: Burrows of colonial burrowing mammals, especially prairie dogs and ground squirrels in open spaces.

NEST: In the West, often nests in colonies in abandoned burrows of prairie dogs, and ground squirrels; also nests in burrows of woodchucks, foxes, badgers, coyotes, and armadillos. In Florida, nests in gopher tortoise burrows. Can excavate own burrow but usually enlarges burrows started by mammals and uses same burrow for years if not disturbed.

FOOD: Hunts by ground foraging, hovering, from a perch, or by flycatching. Primarily eats insects and small mammals, but also takes some birds, fishes, and frogs.

REFERENCES: Butts 1973, Errington and Bennett 1935, Evans 1982, Heintzelman 1979, Karalus and Eckert 1974, Tate and Tate 1982, Terres 1980, Zarn 1974b.

Spotted Owl

Strix occidentalis



L16"

RANGE: Resident from southwestern British Columbia south through western Washington and western Oregon to southern California; also in the mountains of southern Utah, central Colorado, Arizona, New Mexico, and extreme western Texas south into northern Mexico.

STATUS: Rare; habitat is limited due to harvesting of old-growth forests. The Northern Spotted Owl subspecies is federally listed as a threatened species.

HABITAT: Inhabits dense coniferous forests with crown closures of at least 80 percent or mixed woodlands and deeply shaded canyons in coastal and mountainous areas of the West. In California, prefers dense fir or Douglas-fir forests on sheer, heavily wooded cliffsides or in narrow canyons, but also inhabits stream valleys well grown with oaks, sycamores, willows, cottonwoods, and alder tangles. In Southwest, favors forested mountain tablelands and canyons from 5,500 to 9,000 feet with dense aspen clumps and creek fringe maples.

SPECIAL HABITAT REQUIREMENTS: Cavities for nesting and at least 600 acres of dense, old-growth forest or deep, narrow, well-wooded canyons per pair.

NEST: Generally nests in cool, shaded areas with well-developed understory and near water. Prefers natural cavities in the old-growth trees, especially Douglas-fir or oaks, with broken tops and infested with mistletoe. Also will nest in cliff cavities, cave floors, occasionally abandoned hawk or raven nests, and hollow logs on the ground. Rarely builds its own nest in the crotch of a tall tree.

FOOD: Preys on a wide variety of animals, but mainly takes small mammals; also eats small birds and large insects.

REFERENCES: Heintzelman 1979, Karalus and Eckert 1974, Marshall 1942, Tate and Tate 1982, Zarn 1974c.

Barred Owl

Strix varia



L17"

RANGE: Resident from southern and eastern British Columbia, northern Washington, and extreme northwestern Montana east to central Saskatchewan, and from southern Manitoba and central Ontario to New Brunswick and Nova Scotia, south to central and southern Texas, the Gulf Coast, southern Florida, and northern Mexico. Northernmost populations are partially migratory.

STATUS: Common to uncommon.

HABITAT: Prefers dense woodlands bordering lakes, streams, swamps, marshes, or low meadows. Favors oak woodlands or mixed forests free of a dense understory but also inhabits deciduous, coniferous, and mixed forests. May also inhabit isolated woodlots with numerous mature trees.

SPECIAL HABITAT REQUIREMENTS: Cool, damp lowlands with large cavity trees 20 inches dbh or greater for nesting.

NEST: Typically nests in a large cavity in a dead tree; may nest in abandoned hawk, crow, or squirrel nests if cavities are scarce. Generally chooses tall, old trees with cavities at least 25 feet above the ground, and in the forest interior. May use the same nest site for many years.

FOOD: Hunts for prey over open fields, clearings, and wetlands near woodlands. Feeds on a wide variety of animals, especially mice and other small mammals; also eats birds (from warblers to grouse and other species of owls), fishes, frogs, salamanders, lizards, snakes, crayfish, scorpions, snails, spiders, and large insects.

REFERENCES: DeGraff et al. 1980, Dunstan and Sample 1972, Heintzelman 1979, Johnsgard 1979, Karalus and Eckert 1974, Nicholls and Warner 1972.

Great Gray Owl

Strix nebulosa



L22"

RANGE: Breeds from central Alaska and northern Yukon to northern Manitoba and northern Ontario, south locally to central California, northern Idaho, northwestern Wyoming, central Saskatchewan, northern Minnesota, and south-central Ontario. Winters generally through the breeding range, wandering south irregularly to the northern tier of States.

STATUS: Locally common to rare.

HABITAT: Inhabits dense coniferous forests in Canada, and montane coniferous forests of the western States. Usually prefers pine and fir forests, rarely straying far out onto tundra barrens and muskeg marshes. Nests in mature poplar woodlands, preferably near muskeg areas, well secluded from human activities, and in spruce stands with islands of tamarack. In winter, may inhabit forests, sparse woodland edges bordering open fields, weedy fields with posts or scattered low trees or bushes, or brackish tidal meadows.

SPECIAL HABITAT REQUIREMENTS: Old hawk or crow nests high in trees.

NEST: Does not build its own nest but uses old nests of goshawks, red-tailed hawks, other large hawks, crows, ravens, or artificial nests. Locates nests 10 to 100 feet high in tamarack, balsam poplar, aspen, and spruce trees.

FOOD: Preys primarily on small mammals but also takes some birds up to the size of a grouse.

REFERENCES: Godfrey 1967, Heintzelman 1979, Johnsgard 1979, Karalus and Eckert 1974, Nero 1980.

Long-eared Owl

Asio otus



L13"

RANGE: Breeds from northern Yukon, southwestern Mackenzie, northern Saskatchewan and Nova Scotia, south to northern Baja California, southern Arizona, western and central Texas, Arkansas, northern Ohio, western Virginia, and New England. Winters from southern Canada south to Baja California, Mexico, southern Texas, the Gulf Coast, and Georgia; casually to Florida.

STATUS: Locally common.

HABITAT: Often inhabits coniferous woodlands but also deciduous forests and forested areas near open country. Also will inhabit open or dense woodlands, parks, orchards, woodlots, wooded swamps, streams, and reservoir shorelines, even low-growing scrub if it is in the form of dense, tangled thickets. Occurs up to 10,000 feet.

SPECIAL HABITAT REQUIREMENTS: Dense vegetation for nesting and roosting cover.

NEST: Most often uses old nests of large birds such as crows, hawks, ravens, herons, or magpies, but will use squirrel nests and natural tree cavities. Usually locates nest 15 to 30 feet above the ground, but may nest on the ground or on ledges. Rarely, will construct own nest.

FOOD: Forages over wooded and open country, preying primarily on mice and other small mammals. Also eats some bats, cottontails, small birds, frogs, small snakes, and insects.

REFERENCES: Armstrong 1958, DeGraff et al. 1980, Heintzelman 1979, Johnsgard 1979, Karalus and Eckert 1974.

Short-eared Owl

Asio flammeus

L13"



RANGE: Breeds from northern Alaska and northern Yukon to northern Quebec and Labrador, south to central California, northern Nevada, Utah, Kansas, Missouri, northern Ohio, northern Virginia, and New Jersey. Winters generally in the breeding range from southern Canada south to Mexico.

STATUS: Locally common; population is declining across southern portions of its range.

HABITAT: Primarily inhabits marshland and open grasslands, but also tundra, open fields, forest clearings, sagelands, deserts, pastures, prairies, lower mountain slopes, canyons, arroyos, dunes, meadows, and other open habitats. In winter, prefers open areas with little or no snow.

SPECIAL HABITAT REQUIREMENTS: Extensive open grasslands with an abundance of rodents.

NEST: Nests are sometimes in small loose colonies, placed in slight depressions on the ground, either in exposed situations or in grassy cover among clumps of weeds or grasses. Rarely, will nest in an excavated burrow.

FOOD: Preys primarily on small mammals, especially voles; also eats birds, bats, and large insects.

REFERENCES: Clark 1975, DeGraff et al. 1980, Heintzelman 1979, Johnsgard 1979, Karalus and Eckert 1974, Low and Mansell 1983, Tate and Tate 1982.

Boreal Owl

Aegolius funereus

L10"



RANGE: Breeds from central Alaska and central Yukon to central Quebec and Labrador, south to northern British Columbia and central Alberta, across to northeastern Minnesota, western and central Ontario, southern Quebec and New Brunswick; also to central Colorado and northeastern Wyoming in the Rocky Mountains.

STATUS: Local and uncommon in United States.

HABITAT: Occurs in mixed coniferous-hardwood forests, but prefers extensive growth of stunted spruce in close proximity to open grasslands. Also inhabits dense alder thickets and forest edges.

SPECIAL HABITAT REQUIREMENTS: Abandoned woodpecker holes in dead or live trees for nesting.

NEST: Prefers abandoned northern flicker or pileated woodpecker cavities in conifers, but will also nest in woodpecker holes in deciduous trees. Usually locates nest 10 to 25 feet above the ground. Sometimes nests in natural cavities and rarely in abandoned bird nests.

FOOD: Preys primarily on small mammals such as lemmings, voles, and mice. Also eats insects, bats, some frogs, salamanders, small snakes and lizards, and during the nesting season, a few birds.

REFERENCES: Heintzelman 1979, Karalus and Eckert 1974.

Northern Saw-whet Owl

Aegolius acadicus
(formerly Saw-whet Owl)



L7"

RANGE: Breeds from southern Alaska, central British Columbia, and central Alberta to southern Quebec and northern New Brunswick, south to southern California, central Mexico, extreme western Texas, central Missouri, southern Wisconsin, central Ohio, West Virginia, and New York; also in the mountains of eastern Tennessee and western North Carolina. Winters generally throughout the breeding range, south irregularly to southern Arizona, the Gulf Coast, and central Florida.

STATUS: Uncommon.

HABITAT: Favors dense woods, especially swampy areas of coniferous or hardwood forests. Also inhabits tamarack bogs, alder thickets, cedar groves, woodlots, and roadside shade trees; may take up temporary residence in or around a barn. Prefers cedar groves and vine clusters for roosting.

SPECIAL HABITAT REQUIREMENTS: Tree cavities large enough for nesting and roosting.

NEST: Usually nests in abandoned nest holes of northern flickers, hairy woodpeckers, or other woodpeckers but will use natural cavities of suitable size. Usually nests 20 to 40 (range 14 to 60) feet above the ground. Occasionally uses nest boxes with a layer of straw or sawdust.

FOOD: Mostly eats small mammals; also preys on small birds, some insects, and frogs.

REFERENCES: DeGraff et al. 1980, Heintzelman 1979, Johnsgard 1979, Karalus and Eckert 1974.

Lesser Nighthawk

Chordeiles acutipennis



L 8" W 21"

RANGE: Breeds from central interior California, southern Nevada, extreme southwestern Utah, central Arizona, central New Mexico, and central and southeastern Texas south to South America. Winters from Mexico south to South America.

STATUS: Common.

HABITAT: Inhabits bare or somewhat brushy country in low deserts of the Southwest. Occurs around dry fields, dry washes and riverbeds; sandy flats, and broad, rocky, sparsely vegetated valleys.

NEST: Generally lays eggs on bare ground in open sandy or gravelly areas but also in brushy areas, lowlands, hills, canyons, and dry rocky slopes and mesas, or on flat gravel and asphalt roofs.

FOOD: Favors areas with concentrations of flying insects, near trees and brush along springs and streams; catches a variety of insects in flight, including winged ants, mosquitoes, June bugs, beetles, moths, and grasshoppers.

REFERENCES: Bent 1940b, Harrison 1979, Oberholser 1974a, Terres 1980.

Common Nighthawk

Chordeiles minor



L 9" W 23"

RANGE: Breeds from southern Yukon and southern Mackenzie to central Quebec and southern Labrador, south to southern California, southern Nevada, southern Arizona, Texas, the Gulf Coast, Florida, Mexico, and Central America. Winters in South America.

STATUS: Common; population is declining in some regions.

HABITAT: Inhabits varied habitats throughout most of North America. Prefers open habitats such as grasslands, sparse woods, or towns and cities. Also inhabits areas with plowed fields, and gravel beaches, as well as railroad right-of-ways and barren areas with rocky soils.

NEST: Lays eggs on flat substrates such as gravelly ground, burned-over areas, gravel and asphalt rooftops, dry barren plains, bare rock, and partially vegetated soil, but always in the open.

FOOD: Mainly crepuscular and nocturnal; sweeps flying insects, from tiny gnats to large moths, out of the air. Eats large quantities of mosquitoes and flying ants as well as beetles, plant lice, grasshoppers, locusts, horseflies, and other insects.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Tate and Tate 1982, Terres 1980.

Common Pauraque

Nyctidromus albicollis
(formerly Pauraque)



L 11"

RANGE: Resident in southern Texas south to South America.

STATUS: Common.

HABITAT: During the breeding season inhabits brushy woods, open chaparral, rivers that are lined by trees and brush. Prefers patches of mesquite and ebony blackbead woodlands. In winter, prefers dense bottomland thickets.

NEST: Lays eggs on the ground in open woodlands with a leaf-covered floor, in brush, or on the edges of fields. Does not build a nest, but in more open areas may conceal eggs by a bush.

FOOD: Usually perches on ground and flies up to snatch airborne insects; sometimes perches on low dead limbs or on top of a bush to hunt for insects. Eats low-flying moths, beetles, locusts, bugs, bees, wasps, butterflies, and other insects.

REFERENCES: Bent 1940a, Harrison 1979, Oberholser 1974a.

Common Poorwill

Phalaenoptilus nuttallii
(formerly Poor-will)



L 7"

RANGE: Breeds from southern interior British Columbia, Montana, southeastern Alberta, and southwestern South Dakota south to Baja California, central Mexico, and central Texas and east to eastern Kansas. Winters in southern portion of breeding range.

STATUS: Common.

HABITAT: Inhabits a variety of arid and semiarid habitats in the West, from lowlands up to 8,000 to 10,000 feet on mountain slopes. Inhabits sparse desert brushland, open prairies, open pinyon-juniper woodlands, mixed chaparral-grassland, brushy rocky canyons, mountain scrub, and pine-oak woodlands. Seems to prefer rocky habitats with scrubby cover or xeric woodlands.

NEST: Lays eggs on gravelly ground or on a flat rock, or in a slight hollow scraped in the ground. Often lays eggs so that they are partially shaded by a bush, weeds, or a tuft of grass.

FOOD: Catches insects such as moths, beetles, chinch bugs, locusts, and grasshoppers by leaping from the ground or a perch, or by picking them up from the ground.

REFERENCES: Bent 1940a, Bevier in Farrand 1983b, Oberholser 1974a, Terres 1980.

Chuck-will's-widow

Caprimulgus carolinensis



L 11"

RANGE: Breeds from eastern Kansas, southern Iowa, and central Illinois to New Jersey and southern New York, south to south-central and southeastern Texas, the Gulf Coast, and southern Florida. Winters from southeastern Texas, Louisiana, and northern Florida to South America.

STATUS: Locally common.

HABITAT: Prefers mixed oak and pine forests, but also inhabits evergreen oak groves, forest edges, and woodlands along river courses. During migration and in winter, frequents open woodland and scrub and palmetto thickets.

NEST: Lays eggs on the ground on dead leaves, usually at the edges of forests, near roads or other clearings, usually with little or no undergrowth around the eggs.

FOOD: Forages at night by flying along edges of woods and fields, catching night-flying moths, beetles, and other insects. Rarely captures small birds such as hummingbirds, warblers, and sparrows and swallows them whole.

REFERENCES: Bent 1940a, Forbush and May 1955, Johnsgard 1979, Sykes in Farrand 1983b, Terres 1980.

Whip-poor-will

Caprimulgus vociferus



L 9"

RANGE: Breeds from north-central Saskatchewan and southern Manitoba to southern Quebec and Nova Scotia, south to eastern Kansas, northeastern Texas, and northern Louisiana across to central Georgia; and from southern California, southern Nevada, central Arizona, and extreme western Texas south to Mexico. Winters from southern Texas, the Gulf Coast, and east-central South Carolina south to Central America.

STATUS: Common; population is declining slightly throughout the breeding range.

HABITAT: In the East, prefers open hardwood or mixed woodlands of pine, oak, and beech, particularly younger stands in fairly dry habitats; also favors stands with scattered clearings. In the Southwest, frequents densely wooded slopes of oak and pine in canyons and mountains.

NEST: Lays eggs on dead leaves on well-drained ground, usually in areas of partial shade where there is no undergrowth. Often nests among trees at the edge of a clearing or path, sometimes laying eggs in the shade of a small bush.

FOOD: Feeds nocturnally, often pursuing insects attracted to lights near buildings in rural areas. Feeds in flight on moths, beetles, mosquitoes, ants, grasshoppers, June bugs, gnats, and other insects.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Raynor 1941, Tate and Tate 1982, Terres 1980.

Black Swift

Cypseloides niger



L 7"

RANGE: Breeds locally from southeastern Alaska, northwestern and central British Columbia, and southwestern Alberta south through the Pacific states and Mexico to Central America; also in northwestern Montana, Colorado, and central Utah. Winters in Mexico and Central America.

STATUS: Rare or uncommon.

HABITAT: Found in areas with rocky cliffs available for nesting, varying from ocean cliffs to mountain ledges, at elevations from sea level to 11,000 feet.

SPECIAL HABITAT REQUIREMENTS: Crevices or ledges on rocky cliffs for nesting, preferably near or behind a waterfall.

NEST: Nests in small colonies, from 5 to 15 pairs, on a sea cliff, ledge, or cave, or in a crevice or ledge on a sheer, high, moist cliff face near or behind a waterfall, or over a pool.

FOOD: Feeds exclusively on insects captured, usually high in the air, during long-distance foraging flights over all types of terrain. It eats various flies, midges, beetles, termites, flying ants, aphids, bees, wasps, and some spiders.

REFERENCES: Bailey and Niedrach 1965, Lack 1956, Terres 1980, Verner and Boss 1980.

Chimney Swift

Chaetura pelagica



L 5" W 12½"

RANGE: Breeds east of the Rocky Mountains from east-central Saskatchewan and southern Manitoba to southern Quebec and New Brunswick, south to eastern New Mexico, south-central and southern Texas, the Gulf Coast and south-central Florida. Winters in South America.

STATUS: Common.

HABITAT: Not confined to any single habitat, as breeding range is largely dependent on suitable nesting sites. Formerly found in habitats with mature, hollow trees, now occurs primarily in the vicinity of buildings in towns, cities, and around farms.

SPECIAL HABITAT REQUIREMENTS: Hollow trees or structures such as chimneys, silos, cisterns, wells, rafters, and airshafts for nest sites.

NEST: Originally adapted to nesting in caves and tree hollows, now mostly nests in man-made structures. Prefers dark areas and sheltered sites high above the ground. Constructs nest of twigs glued together with saliva; attaches nest to a vertical wall anywhere from near the top of a structure to more than 20 feet below the top.

FOOD: Forages almost entirely on flying insects including beetles, flies, ants, termites, and bugs but will sometimes take small caterpillars hanging from tree branches or leaves.

REFERENCES: Bailey and Niedrach 1965, DeGraff et al. 1980, Fischer 1958, Forbush and May 1955, Johnsgard 1979, Terres 1980.

Vaux's Swift

Chaetura vauxi



L 4½"

RANGE: Breeds from southeastern Alaska, northwestern and southern British Columbia, northern Idaho, and western Montana south, chiefly from the Cascades and Sierra Nevada westward, to central California south to northern Mexico. Winters in Central America.

STATUS: Uncommon.

HABITAT: Inhabits forested regions with large trees. In Montana, it occurs in mixed forests of Douglas-fir, ponderosa pine, lowland fir, western larch, yellow birch, aspen, and cottonwoods; in California, inhabits ponderosa pine, mixed conifer, and Jeffrey pine forests, and possibly black oak woodlands. Also inhabits river valleys in dense Douglas-fir and redwood forests.

SPECIAL HABITAT REQUIREMENTS: Hollow stubs or snags for nesting.

NEST: Nests are usually in a tall, hollow, dead tree, or inside burned-out stumps, generally within 20 inches but up to 6 feet up from the bottom of the cavity. Also nests in chimneys, but is not dependent upon them.

FOOD: Feeds exclusively on flying insects captured in mid-air in forest openings, especially over lakeshores and streams.

REFERENCES: Baldwin and Hunter 1963, Baldwin and Zaczkowski 1963, Bent 1940b, Scott et al. 1977, Terres 1980, Verner and Boss 1980.

White-throated Swift

Aeronutes saxatalis



L 6½" W 14"

RANGE: Breeds from southern British Columbia, Idaho, Montana, and southwestern South Dakota south through the Pacific and southwestern States to Baja California, Mexico, and Central America, and east to western Nebraska and western Texas. Winters from central California, central Arizona and, rarely, southern New Mexico south to Central America.

STATUS: Common.

HABITAT: Inhabits areas with steep cliffs and deep canyons at elevations from near sea level to about 13,000 feet. Inhabits primarily mountainous country but also coastal cliffs, rugged foothills, and desert canyons; ranges over adjacent valleys while foraging.

SPECIAL HABITAT REQUIREMENTS: Crevices in cliffs for nesting.

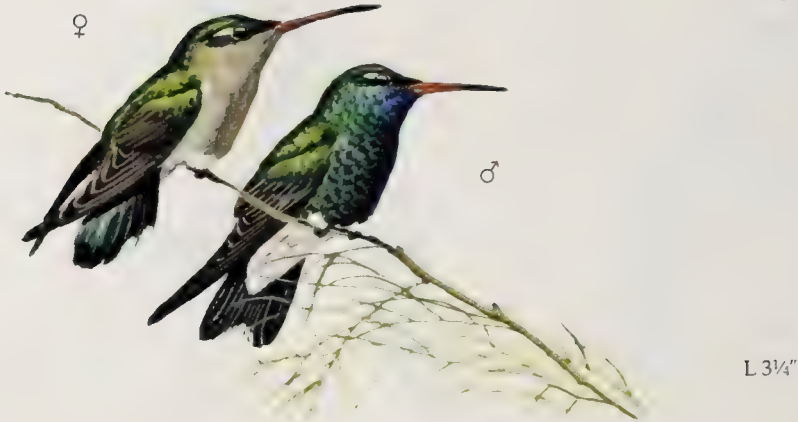
NEST: Places nests in deep cracks and crevices in steep, rocky, often inaccessible cliff faces or canyons, from 10 to 200 feet or more above the base. Sometimes nests in cracks of building walls.

FOOD: Feeds on flying insects captured over any terrain while flying swiftly, usually high above the ground. Eats flies, beetles, bees, wasps, ants, bugs, leafhoppers, and other insects.

REFERENCES: Bailey and Niedrach 1965, Bent 1940b, Terres 1980, Verner and Boss 1980.

Broad-billed Hummingbird

Cynanthus latirostris



RANGE: Breeds from southeastern Arizona, southwestern New Mexico, and very locally in western Texas south through Mexico. Winters in Mexico, casually north to southern Arizona.

STATUS: Common.

HABITAT: Prefers desert mountain canyons, riparian woodlands, and higher desert washes, especially where sycamores, cottonwoods, willows, and mesquite are present.

SPECIAL HABITAT REQUIREMENTS: Red or red and yellow flowers for nectar.

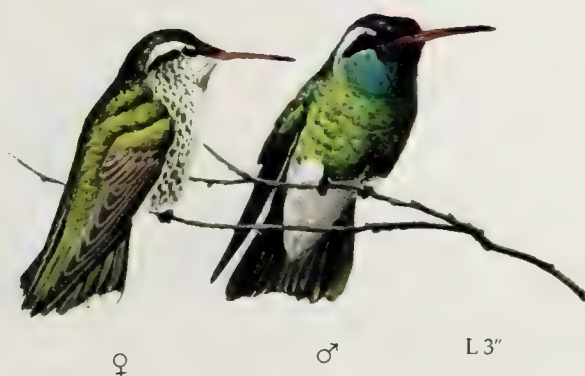
NEST: Places nest on a branch of a small tree, or a stalk of a vine or shrub, usually 4 to 7 feet above the ground.

FOOD: Prefers to feed on nectar from red, or red and yellow flowers such as ocotillo, paintbrushes, and others. Also gleans small insects and spiders from the undersides of branches and leaves.

REFERENCES: Cottam and Knappen 1939, Johnsgard 1983b, Moore 1939, Terres 1980, Terrill in Farrand 1983b.

White-eared Hummingbird

Hylocharis leucotis



RANGE: Resident from Sonora, Chihuahua, Coahuila, Nuevo Leon, and Tamaulipas south through the highlands of Mexico, Guatemala, El Salvador, and Honduras to north-central Nicaragua. Irregularly, in summer, in the mountains of southern Arizona, southwestern New Mexico, and western Texas; northernmost populations are partially migratory.

STATUS: Rare and irregular in United States.

HABITAT: Prefers the undergrowth of oak forests but also occurs in pine woods, dense pine-oak forests, high mountain fir forests, partially open mountain country with scattered trees and shrubs, suburban gardens, and vacant lots with scattered shrubs and flowers. (Little is known about its habits in the United States, and there is no good evidence that it has ever nested in Arizona.)

SPECIAL HABITAT REQUIREMENTS: Flowers, especially blue flowers such as salvia, for nectar.

NEST: Nest sites are nearly always in shrubs or fairly low trees.

FOOD: Feeds on flies and other insects found in honeysuckle and other flowers. Is easily attracted to hummingbird feeders.

REFERENCES: Cottam and Knappen 1939, Johnsgard 1983b, Phillips et al. 1964, Terres 1980, Terrill in Farrand 1983b.

Buff-bellied Hummingbird

Amazilia yucatanensis



L 3¾"

RANGE: Resident from southern Texas in the lower Rio Grande Valley south to Honduras. Casual north to central and eastern Texas, and southern Louisiana.

STATUS: Uncommon; once common, but has largely disappeared north of the border, probably as a result of habitat destruction and the spraying of insecticides.

HABITAT: Inhabits semiarid lowlands dominated by woods or scrubby growth, preferring dense thickets, flowering bushes, and tangled vines along the banks of streams and ponds, resacas, and gullies. Also occurs in semiarid coastal scrub in open woods, chaparral thickets, farms and gardens, and in citrus groves.

SPECIAL HABITAT REQUIREMENTS: Flowers for nectar.

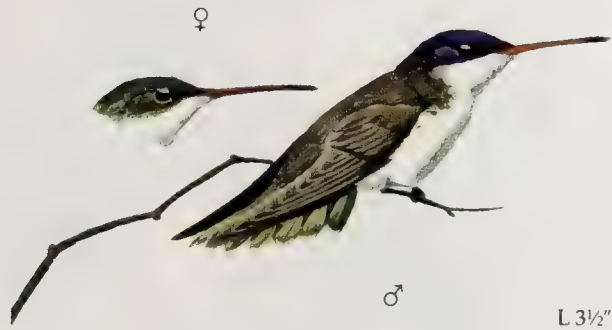
NEST: Places nest 3 to 8 feet above the ground on a small drooping limb or horizontal fork of a twig in a small tree or bush such as anacahuita, ebony blackbead, or hackberry, but sometimes in willow. Often chooses a nest site that is near a road, trail, or other clearing.

FOOD: Feeds on the nectar of native flowers and eats insects.

REFERENCES: Johnsgard 1983b, Oberholser 1974a, Terres 1980.

Violet-crowned Hummingbird

Amazilia violiceps



RANGE: Breeds in southern Arizona in the Huachuca and Chiricahua mountains, and in southwestern New Mexico in Guadalupe Canyon south to central Mexico. Casual in southern California. With a few exceptions, withdraws into Mexico in winter.

STATUS: Rare and local; first discovered breeding in the United States in 1959.

HABITAT: Prefers riparian sycamore groves in desert mountain canyons. In the United States, generally associated with streamside plant life in the deserts and foothills of mountains.

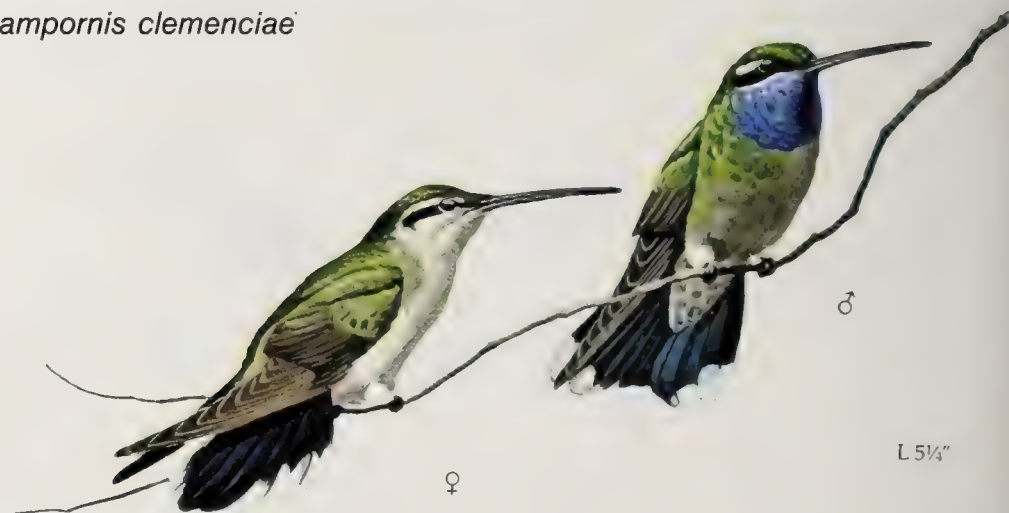
NEST: Builds a nest that is saddled to a horizontal limb in sycamores, 25 to 40 feet above the ground.

FOOD: Probably consumes nectar and insects but no definitive reports have been published.

REFERENCES: Johnsgard 1983b, Phillips et al. 1964, Terres 1980, Terrill in Farrand 1983b, Zimmerman and Levy 1960.

Blue-throated Hummingbird

Lampornis clemenciae



RANGE: Breeds in southeastern Arizona in the Huachuca and Chiricahua Mountains, and from western Texas south to Oaxaca. Casual north to Colorado. Winters in Mexico, but occurs casually at Arizona feeders.

STATUS: Fairly common to uncommon.

HABITAT: Inhabits lush vegetation along wooded streamsides in mountain canyons. In Texas, found among baldcypress, pines, oaks, and bigtooth maples from 4,900 to 7,500 feet in elevation.

SPECIAL HABITAT REQUIREMENTS: Nest sites that are sheltered from rain and sunlight, near an abundance of flowers for feeding, and within a few feet of a stream.

NEST: Builds nest in sites that are completely covered from above, such as in vertical-walled canyons, rock overhangs, on plant stalks, under eaves of buildings, bridges, water towers, and inside buildings. May use the same nest site for several years, adding to the nest each time it is used.

FOOD: Forages on drier canyon slopes to feed on nectar of agave and honeysuckle flowers; also frequents flower gardens. Also eats flies, bugs, small beetles, wasps, spiders, daddy-longlegs, and pollen.

REFERENCES: Cottam and Knappen 1939, Johnsgard 1983b, Oberholser 1974a, Terres 1980, Terrill in Farrand 1983b.

Magnificent Hummingbird

Eugenes fulgens
(formerly Rivoli's Hummingbird)



RANGE: Breeds in western Colorado, and from southeastern Arizona, southwestern New Mexico, and western Texas south to Panama. Winters in Mexico and Central America, though a few remain at Arizona feeders.

STATUS: Rare in Colorado, elsewhere uncommon to common.

HABITAT: Found above 5,000 feet in deciduous woods along streams, and in pine or oak woods on mountain slopes and ridges.

SPECIAL HABITAT REQUIREMENTS: Flowers for nectar.

NEST: Builds nest on a horizontal branch from 20 to 55 feet above the ground. Uses a variety of trees for nesting, including cottonwoods, mountain maples, sycamores, alders, walnuts, pines, and Douglas-fir.

FOOD: Visits flowers for nectar, including those of agave, iris, and bright-red salvia. Also eats leaf bugs, aphids, leafhoppers, parasitic wasps, beetles, flies, moths, and spiders.

REFERENCES: Cottam and Knappen 1939, Johnsgard 1983b, Kaufman in Farrand 1983b, Terres 1980.

Lucifer Hummingbird

Calothorax lucifer



RANGE: Breeds from southern Arizona and the Chisos Mountains of western Texas south to the highlands of Mexico. Winters in Mexico.

STATUS: Rare and local.

HABITAT: Inhabits cactus-covered slopes, dry canyons, arid mesas, and foothills and semi-desert habitats from 4,000 to 7,400 feet, often where century-plant agaves are abundant.

SPECIAL HABITAT REQUIREMENTS: Flowers for nectar, particularly agaves.

NEST: Places nest in a shrub or on a seed pod of a dead stalk of an agave, 4 to 6 feet above the ground.

FOOD: Forages on Chisos bluebonnet, ocotillo, tree tobacco, and yellow-green blossoms of agave for nectar; probably consumes a high proportion of insects as well.

REFERENCES: Garrett in Farrand 1983b, Johnsgard 1983b, Oberholser 1974a, Terres 1980.

Ruby-throated Hummingbird

Archilochus colubris

L 3"



RANGE: Breeds from central Alberta and central Saskatchewan to southern Quebec and New Brunswick south, east of the Rocky Mountains, to southern Texas, the Gulf Coast, and Florida. Winters from southern Texas south to Central America; also in southern Florida.

STATUS: Common.

HABITAT: Occurs in a variety of wooded habitats, ranging from rather dense to open coniferous and deciduous woodlands, orchards, and shade trees in yards. Also inhabits mixed woodlands, parks, and gardens, often breeding in woodlands near streams or wooded swamps.

SPECIAL HABITAT REQUIREMENTS: Plants that provide tubular nectar-bearing flowers such as honeysuckle, lantana, gilia, and trumpet vine, especially red flowers.

NEST: Places nest 6 to 50 feet, typically 10 to 20 feet, above the ground, on a fairly level or downward slanting twig or branch protected from above by larger branches or a leafy canopy. Often locates nest near or sometimes directly over water, or near a woodland trail. Uses a variety of trees for nesting, but appears to favor hardwoods over conifers, especially those with rough, lichen-covered bark. May use the same nest site year after year.

FOOD: Consumes nectar from flowers, especially red, orange, and pink ones. Also eats small insects, spiders, and tree sap.

REFERENCES: Beal and McAtee 1912, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, 1983b, Terres 1980.

Black-chinned Hummingbird

Archilochus alexandri

L 3"



RANGE: Breeds from southwestern British Columbia and northwestern Montana south to Baja California, southern Texas, and northern Mexico, and east to western Wyoming, eastern Colorado, eastern New Mexico, and central Texas. Winters in Mexico, casually to southern Texas, southern Louisiana, northwestern Florida, and southern California.

STATUS: Common.

HABITAT: Found most frequently in arid regions, where it inhabits oak and riparian woodlands of canyons and lowlands, small patches of willows along dry washes, chaparral, pine-oak woodlands, orchards, and parks. Prefers sites with a low percentage of canopy cover.

SPECIAL HABITAT REQUIREMENTS: Flowers for nectar.

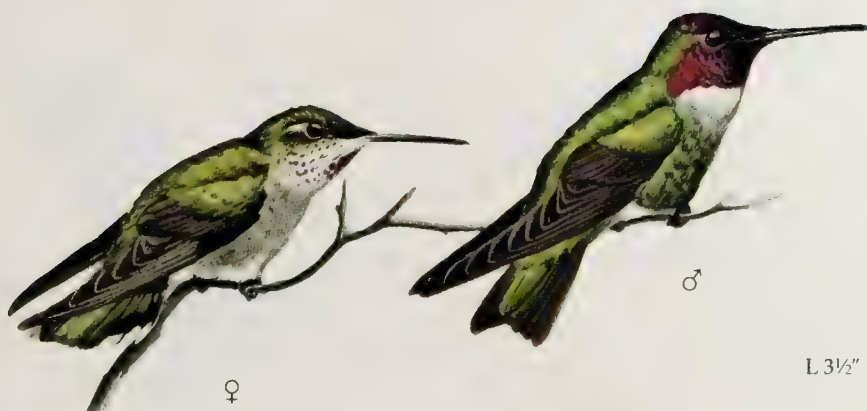
NEST: Usually places nest 4 to 8 feet (but up to 30 feet) above the ground, on a small drooping branch or in a fork of a small tree or shrub, near or overhanging a stream, spring, or dry creek bed. Prefers to nest in oaks, but also nests in alders, cottonwoods, sycamores, laurel, willows, apple, and orange trees in orchards, and in woody vines and tall herbaceous weeds.

FOOD: Feeds on nectar from flowers. Also gleans insects from foliage, and hawks for flying insects.

REFERENCES: Bent 1940b, Harrison 1979, Johnsgard 1983b, Phillips et al. 1964, Terres 1980, Verner and Boss 1980.

Anna's Hummingbird

Calypte anna



RANGE: Breeds in western Washington, western Oregon, California, and southern Arizona. Nonbreeding birds occur regularly north to southern British Columbia and, rarely, east to western Texas. Winters from southwestern Oregon south to Mexico, and east to southern Arizona.

STATUS: Common.

HABITAT: Typically in habitats such as chaparral-covered hillsides, canyons, and mountain slopes and oak or sycamore woodlands in canyon bottoms. Also inhabits open mixed woodlands and chaparral, parks, and gardens from sea level to 5,900 feet, preferring timbered sites with sparse canopy cover.

SPECIAL HABITAT REQUIREMENTS: Flowers for nectar near the nest site, and forest openings.

NEST: Places nest on a variety of substrates, including trees such as citrus, eucalyptus, and oaks, as well as chaparral bushes and vines at heights ranging from less than 3 to 30 feet.

FOOD: Obtains nectar from many flowering plants. Also eats flies, bees, wasps, bugs, and spiders gleaned from flowers and foliage and hawked from the air.

REFERENCES: Beal and McAtee 1912, Grinnell and Miller 1944, Johnsgard 1983b, Stiles 1973, Verner and Boss 1980.

Costa's Hummingbird

Calypte costae



RANGE: Breeds from central California, southern Nevada, and southwestern Utah south to southern Arizona and Mexico. Winters from southern California and southern Arizona south to Mexico.

STATUS: Common.

HABITAT: In southwestern deserts, frequents arid washes and hillsides, dry chaparral, and suburban areas where exotic plants have been introduced. In California, inhabits washes, mesas, and hillsides, particularly where sages, ocotillo, yuccas, and cholla cacti are abundant. Relatively independent of water during the breeding season, and thus occupies drier habitats than other hummingbirds.

SPECIAL HABITAT REQUIREMENTS: Flowering plants for nectar.

NEST: Builds nests in a variety of sites, usually from 1 to 9 feet above the ground, on twigs or limbs of oaks, alders, hackberry, willow, palm, citrus trees in open orchards, or other trees; in sage, dead yuccas, branching cacti, and paloverde; or on vines clinging to rock faces.

FOOD: Obtains nectar and insects from a variety of flowering desert plants; also eats spiders.

REFERENCES: Garrett in Farrand 1983b, Grinnell and Miller 1944, Johnsgard 1983b, Terres 1980.

Calliope Hummingbird

Stellula calliope



RANGE: Breeds in the mountains from central interior British Columbia and southwestern Alberta south to Baja California, and east to northern Wyoming and western Colorado. Winters in Mexico.

STATUS: Uncommon.

HABITAT: Frequents meadows and canyons; riparian aspen, willow, and alder thickets; and other brushy areas within the coniferous forests of western mountains. Occupies a broad vertical range during the breeding season, from 600 feet in the northern portions of its range to 11,500 feet in the Sierra Nevada. Prefers timbered stands near water with a low to intermediate canopy cover.

SPECIAL HABITAT REQUIREMENTS: Flowers, preferably red, for nectar.

NEST: Typically locates nest below a larger branch or canopy of foliage, usually on a branch that has small knots of dead, black or gray mistletoe or pine cones which nest strongly resembles. Locates nest 2 to 70 feet above ground, frequently in a riparian area. May use the same site in subsequent years.

FOOD: Obtains nectar from a variety of flowers, preferring red ones. Hawks for small flying insects, and eats spiders.

REFERENCES: Bent 1940b, Calder 1971, Garrett in Farrand 1983b, Johnsgard 1983b, Terres 1980, Verner and Boss 1980.

L 3¾"



Broad-tailed Hummingbird

Selasphorus platycercus

RANGE: Breeds in the mountains from north-central Idaho, northern Utah, and northern Wyoming south to southeastern California, northern Mexico, and western Texas. Winters in Mexico.

STATUS: Common.

HABITAT: Inhabits meadows and patches of flowers within pine, spruce, fir, and sometimes aspen forests from 4,000 to 11,000 feet. Also inhabits gardens in towns and cities, and sometimes ranges eastward onto the Plains.

SPECIAL HABITAT REQUIREMENTS: Flowers for nectar.

NEST: Nests are saddled on large horizontal limbs or small twigs in shrubs along moist canyon walls, in Douglas-fir, ponderosa pine, subalpine fir, or other conifer, oak, aspen, alder, willow, or cottonwood. Usually locates nest 4 to 15 feet above the ground, and frequently uses the same location for several consecutive summers.

FOOD: Obtains nectar from a variety of flowers. Comes to hummingbird feeders for sugar water and eats small insects and spiders.

REFERENCES: Bailey and Niedrach 1965, Bent 1940b, Johnsgard 1979, 1983b, Phillips et al. 1964, Terres 1980.

Rufous Hummingbird

Selasphorus rufus



RANGE: Breeds from southern Alaska, southern Yukon, and western and southern British Columbia to western Montana south, primarily in the mountains, to northwestern California, eastern Oregon, and central Idaho. Winters in Mexico, in small numbers to southern Texas and the Gulf Coast and, rarely, in coastal southern California.

STATUS: Common.

HABITAT: Occurs in northwestern parks and gardens, in chaparral, and in meadows, forest edges, and riparian thickets of coniferous woodlands. During migration, may be found in high mountain meadows as well as in the Pacific lowlands in open areas where flowers are present.

SPECIAL HABITAT REQUIREMENTS: Flowers (especially red) for nectar.

NEST: In northern latitudes, builds nest close to the ground where it is sheltered from wind and cold; otherwise, builds nest 5 to 50 feet above ground. May nest in a variety of sites, sometimes in colonies with up to 20 nests in a small area. Favors the drooping branches of conifers, but also nests in bushes and among vines. Sometimes builds a new nest on top of the previous year's nest.

FOOD: Consumes nectar from flowers, especially red flowers. Also eats insects.

REFERENCES: Bent 1940b, Garrett in Farrand 1983b, Johnsgard 1983b, Terres 1980.

Allen's Hummingbird

Selasphorus sasin



RANGE: Breeds from southwestern Oregon south through coastal California to Santa Barbara County. Resident in southern California in the Channel Islands and on the Palos Verdes Peninsula. Winters in Mexico.

STATUS: Common.

HABITAT: Found within the Pacific coastal fog belt, inhabiting meadows, moist canyon bottoms, humid woody or brushy ravines, brushy edges of coniferous forest, coastal chaparral, and parks.

SPECIAL HABITAT REQUIREMENTS: Shade, preferably patchy, over the nest site, and flowers for nectar.

NEST: Usually builds nest on a site with several separate supports such as a dense tangle of vines. Less frequently, attaches nest to the side of a drooping twig or limb from 1 to 90 feet above the ground in trees such as oaks, eucalyptus, and Monterey cypress, or in shrubs in streamside thickets.

FOOD: Obtains nectar from a variety of flowers. Also hawks for small insects.

REFERENCES: Aldrich 1945, Bent 1940b, Harrison 1979, Terres 1980.

Elegant Trogon

Trogon elegans
(formerly Coppery-tailed Trogon)



L 10"

RANGE: Resident from southern Arizona, primarily in Chiricahua, Huachuca and Atascosa mountains south to Costa Rica. Mostly migratory in northernmost part of range; casual in Arizona, southwestern New Mexico, and southern Texas in winter.

STATUS: Locally fairly common.

HABITAT: Occurs in oak and pine-oak forests in mountain canyons, and in sycamore, walnut, and cottonwood groves along canyon streams.

SPECIAL HABITAT REQUIREMENTS: Natural cavities in trees or large, deserted woodpecker holes.

NEST: Builds nest inside cavities of large streamside trees such as sycamores or cottonwoods, 12 to 40 feet above the ground.

FOOD: Primarily eats insects and some fruits.

REFERENCES: Bent 1940a, Cottam and Knappen 1939, Oberholser 1974a, Terres 1980, Terrill in Farrand 1983b.

Belted Kingfisher

Ceryle alcyon



RANGE: Breeds from western and central Alaska, central Yukon, and western and south-central Mackenzie to central Quebec and east-central Labrador south to southern California, southern Texas, the Gulf Coast, and central Florida. Winters from south-coastal and southeastern Alaska, central and southern British Columbia, and western Montana across to Nebraska, the southern Great Lakes and New England south to South America.

STATUS: Common.

HABITAT: Occurs in the vicinity of ponds, lakes, rivers, and streams, even rocky seacoasts near areas of exposed vertical ground such as bluffs, road cuts, gravel pits, or sandbanks. Prefers small, clear bodies of water to large lakes. In winter, frequents ice-free waters that allow access to food.

SPECIAL HABITAT REQUIREMENTS: Nests preferably within 1 mile of water with low turbidity supporting adequate aquatic animal populations, and perches near water to sight prey.

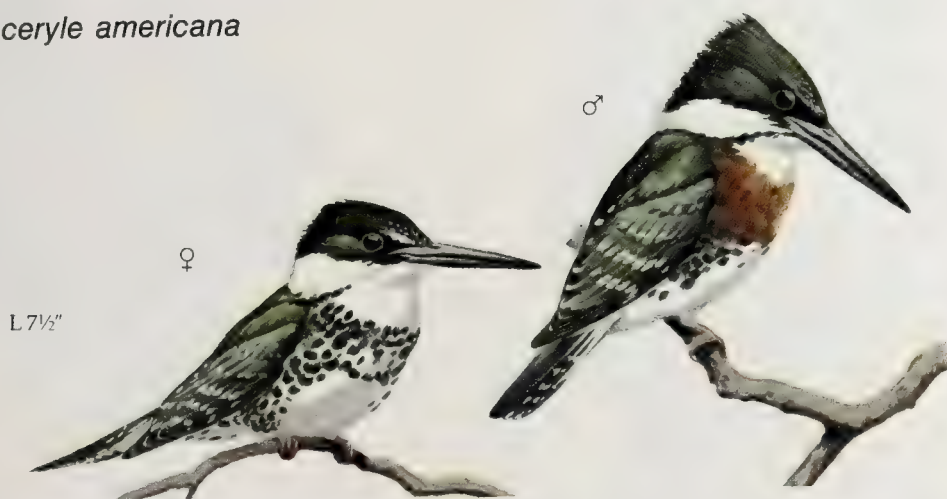
NEST: Typically excavates a nest burrow 3 to 6 feet, up to 15 feet, deep in a bank with sandy, gravelly, or clay soil. Constructs burrow at least 5 feet above level ground or water, and usually within 3 feet of the top of a bank. Occasionally locates burrow far from water, and at times may have to forage up to 5 miles from the nest site. Builds a nest cavity that is an enlarged area at the end of the burrow, often lined with disgorged food pellets.

FOOD: Feeds primarily on fish averaging 3 to 4 inches, caught by diving into water. Forages from a perch or while hovering over water. Also may eat crayfish, mollusks, frogs, tadpoles, lizards, newts, mice, large insects, and occasionally fleshy fruits.

REFERENCES: Cornwall 1963, DeGraff et al. 1980, Johnsgard 1979, Terres 1980, White 1953.

Green Kingfisher

Chloroceryle americana



RANGE: Resident in south-central and southern Texas, occurring up the Rio Grande at least as far as Del Rio, north onto Edwards Plateau, and south through Mexico to South America.

STATUS: Fairly common.

HABITAT: Prefers small, shaded, clear streams and quiet backwaters, but also found around larger bodies of water with dense, low vegetation along the banks.

SPECIAL HABITAT REQUIREMENTS: High banks along clear streams with an abundant supply of small fishes.

NEST: Digs burrow 2 to 3 feet deep near the top of a high bank over water with a small entrance, about 2 to 3 inches in diameter, usually well concealed by trailing plants and vines or dead vegetation draping the top of the bank.

FOOD: Sights small fishes from a low perch of overhanging branches, roots, or rocks, often just inches above water; plunges into the water from the perch to catch the fishes, rarely hovering.

REFERENCES: Bent 1940a, Kaufman in Farrand 1983b, Oberholser 1974a, Terres 1980.

Lewis' Woodpecker

Melanerpes lewis



RANGE: Breeds from southern British Columbia to southwestern South Dakota and northwestern Nebraska south to south-central California, central Arizona, southern New Mexico, and eastern Colorado. Winters from northern Oregon, southern Idaho, central Colorado, and south-central Nebraska south irregularly to northern Baja California, northern Mexico, southern New Mexico, and west Texas.

STATUS: Population has been declining; has been placed on the blue list.

HABITAT: Inhabits open country with scattered trees rather than dense forests; open or parklike ponderosa pine forests are probably the major breeding habitat. Is attracted to burned-over stands of Douglas-fir, mixed conifer, pinyon-juniper, riparian, and oak woodlands but is also found in fringes of pine and juniper tree stands and in deciduous forests, especially riparian cottonwoods. Prefers areas with a good understory of grasses and shrubs to support insect prey populations. Winters over a wide range of habitats, especially where oaks are present.

SPECIAL HABITAT REQUIREMENTS: Dead trees or tall stumps for cavity nests.

NEST: Generally excavates its own nest cavity in dead trees or tall stumps, but will use natural cavities or old excavated nest sites. Nests about equally in coniferous and deciduous trees, but favors ponderosa pine, cottonwood, and sycamore.

FOOD: Primarily eats insects during spring and summer. Catches flying insects by hawking from perches in dead trees or stumps. Mostly eats fruits and berries during fall. Gathers and stores winter food, mostly acorns, in crevices of dead trees, power poles, or oak bark.

REFERENCES: Beal and McAtee 1912, Bock 1970, Johnsgard 1979, MacRoberts and MacRoberts 1976, Oberholser 1974a, Tate and Tate 1982.

Red-headed Woodpecker

Melanerpes erythrocephalus



RANGE: Breeds from southern Saskatchewan, southern Ontario, southern New Hampshire, and southern New Brunswick south to central Texas, the Gulf Coast and Florida, extending west to central Montana, eastern Wyoming, eastern Colorado, and central New Mexico, rarely to northeastern Utah. Winters regularly through the southern two-thirds of the breeding range, rarely or casually north to the limits of the breeding range.

STATUS: Common, but declining in the Southeast.

HABITAT: Inhabits relatively open forests or woodlots with low stem density, preferring savannahlike grasslands with scattered trees and forest edges. Attracted to areas with many dead trees which provide nesting and roosting sites, and lush herbaceous ground cover that produces abundant insect populations. Tends to avoid forests with closed canopies, but will move from forest edges to the interior during winter.

SPECIAL HABITAT REQUIREMENTS: Relatively open forests with dead and dying trees for cavities and feeding perches.

NEST: Nests generally in the trunk of a dead tree but sometimes in a dead limb. Tends to select isolated snags for nesting, especially those without bark.

FOOD: In summer, mostly eats insects caught by hawking from perches in dead trees; stores mast, mainly acorns, beechnuts, and corn, under bark, in cracks, knotholes, and tree cavities for winter use.

REFERENCES: Beal 1911, Conner and Adkisson 1977, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, MacRoberts and MacRoberts 1976, Reller 1972, Tate and Tate 1982.



Acorn Woodpecker

Melanerpes formicivorus

L 8"

RANGE: Resident west of the Cascade and Sierra Nevada Mountains from northwestern Oregon south through California to southern Baja California; and from northern Arizona, northern New Mexico, and western Texas south through the highlands of Central America to Colombia.

STATUS: Common within its range.

HABITAT: Inhabits mixed pine-oak woodlands and adjacent open grasslands along the Pacific Coast and the Southwest.

SPECIAL HABITAT REQUIREMENTS: Oak trees to provide food and large snags that provide sites for nesting, roosting, and food storage.

NEST: Excavates cavities in pine snags, living and dead oaks, sycamores, cottonwoods, and willows for nesting and roosting. May use the same cavity for several years. Nests communally and all birds of a community assist in feeding young.

FOOD: Mostly consumes acorns, which are stored in holes drilled in communal trees. Also consumes sap from oaks from midwinter to summer, and hawks insects when available.

REFERENCES: Beal 1911, MacRoberts 1970, MacRoberts and MacRoberts 1976, Overholser 1974a.

Gila Woodpecker

Melanerpes uropygialis



L 8¼"

RANGE: Resident from southeastern California, extreme southern Nevada, central Arizona, and southwestern New Mexico south through Baja California and western Mexico to Jalisco.

STATUS: Locally common.

HABITAT: Inhabits desert mesas in association with creosotebush, mesquite, and saguaro and organ-pipe cactus. Also occurs in riparian areas and in foothill canyons among cottonwoods, willows, and sycamores.

SPECIAL HABITAT REQUIREMENTS: Suitable nest sites in the Sonoran Desert such as cottonwoods, mesquites, and saguaros.

NEST: Excavates holes mainly in saguaro but uses cottonwoods, willows, and mesquites at higher elevations and in riparian habitat.

FOOD: Mainly eats insects; also eats fruits and nuts, and occasionally preys on nestling birds and eggs.

REFERENCES: Bent 1939, Phillips et al. 1964, Terres 1980.

Golden-fronted Woodpecker

Melanerpes aurifrons



RANGE: Resident from southwestern Oklahoma and north-central Texas south through central Texas to Mexico and Central America.

STATUS: Locally abundant; populations may be declining because of mesquite control programs.

HABITAT: Prefers mesquite and riparian woodlands, but also inhabits semiarid brush country, pecan groves, and upland oak stands.

SPECIAL HABITAT REQUIREMENTS: Trees large enough for nest cavity.

NEST: Excavates nest hole in large living or dead trees, especially in mesquite, oak, and pecan. May also excavate holes in fence posts and telephone or electric poles; occasionally uses bird boxes.

FOOD: Gleans much of its food, which consists of insects, acorns, pecans, wild fruits, corn, and occasionally citrus.

REFERENCES: Bent 1939, Johnsgard 1979, Oberholser 1974a.

Red-bellied Woodpecker

Melanerpes carolinus

L 8½" ♀



RANGE: Resident from southeastern Minnesota, south-central Wisconsin, southern Michigan, southern Ontario, central New York, and Massachusetts south to central Texas, the Gulf Coast, and southern Florida, and west to Iowa, eastern Nebraska, western Kansas, central Oklahoma, and north-central Texas.

STATUS: Common. Range has been expanding westward along the river valleys of the Great Plains.

HABITAT: Inhabits deciduous and coniferous forests of the southeastern United States, especially mature woodlands with dead and broken-topped trees. Also frequents farm woodlots, riparian forests, and orchards.

SPECIAL HABITAT REQUIREMENTS: Mature woodlands with dead trees or trees with large dead limbs for nesting.

NEST: Nests are excavated in a variety of sites, including trees, stumps, dead limbs, and poles. May nest in buildings or in nest boxes usually less than 40 feet above the ground. Prefers relatively soft deciduous tree species and dead trees or those with decayed stubs.

FOOD: Eats mostly vegetable material including fruit, nuts, poison ivy seeds, pine seeds, and juniper berries, but also feeds on some wood-boring insect larvae found in dead wood.

REFERENCES: Beal 1911, DeGraff et al. 1980, Johnsgard 1979, Reller 1972.

Yellow-bellied Sapsucker

Sphyrapicus varius

(includes Red-naped Sapsucker

Sphyrapicus nuchalis)



RANGE: Breeds from eastern Alaska east to central Newfoundland, south to northeastern British Columbia, eastern North Dakota, New Hampshire, and locally in the Appalachians south to eastern Tennessee and western North Carolina; and in the Rocky Mountain region from south-central British Columbia to western Montana south, east of the Cascades, to east-central California and western Texas. Winters from Missouri, the Ohio Valley, and New Jersey south through Texas, southeastern United States to central Panama; in the West from southern California, central Arizona, and central New Mexico south to southern Baja California and Jalisco.

STATUS: Common.

HABITAT: Breeds in deciduous and mixed deciduous-coniferous forests in the eastern and northern parts of its range, especially in woodlands with *Populus*. In the Rocky Mountain region, occurs primarily in aspen forests or in coniferous forests where aspen is present. Uses a variety of forests and open woodlands, parks, and orchards in winter.

SPECIAL HABITAT REQUIREMENTS: Dead or live trees with heartrot for cavity nests.

NEST: Excavates cavities in snags or in live trees with rotten heartwood. Prefers aspens but will nest in ponderosa pine, birch, elm, butternut, cottonwood, alder, willow, beech, maple, and fir. May use the same nest tree for several years, but excavates a new cavity each year.

FOOD: Drills rows of holes (sapwells) through the outer bark and consumes cambium and tree sap. Also eats a variety of insects attracted to the sapwells (ants are probably the dominant animal food). Fruits, mast, and *Rhus* seeds are included in the diet.

REFERENCES: Beal 1911, DeGraff et al. 1980, Howell 1952, Johnsgard 1979, Lawrence 1967, Thomas et al. 1979.

Red-breasted Sapsucker

Sphyrapicus ruber
(split from Yellow-bellied Sapsucker)

L 7¼"



RANGE: Breeds from southeastern Alaska and coastal and central interior British Columbia south, west of the Cascades, to northwestern California, and in the Sierra Nevada to east-central California and extreme western Nevada; locally in the mountains of southern California and southern Nevada. Winters throughout the breeding range (except interior British Columbia) south through most of California (west of the deserts) to Baja California.

STATUS: Locally common.

HABITAT: Breeds in coniferous and conifer-aspen associations including the humid coastal lowlands. Also occurs in open woodlands and parks in winter.

SPECIAL HABITAT REQUIREMENTS: Live or dead trees suitable for cavity nests.

NEST: Apparently excavates a cavity in a variety of tree species, including aspen, alder, cottonwood, fir, willow, and birch.

FOOD: Drills sapwells in a variety of tree species and consumes sap and cambium. Also feeds on a variety of insects, especially ants, and some fruits.

REFERENCES: Beal 1911, Bent 1939.

Williamson's Sapsucker

Sphyrapicus thyroideus



RANGE: Breeds from extreme southern interior British Columbia, Idaho, western Montana, and Wyoming south in the mountains to northern and east-central California, central Arizona, and southern New Mexico. Winters generally from the breeding range south to Baja California, and east to western Texas and Mexico.

STATUS: Common.

HABITAT: Prefers mixed conifer-hardwood forests in the Rocky Mountain region but also inhabits the subalpine spruce-fir-lodgepole zone, and ponderosa pine, Douglas-fir, and aspen forests.

SPECIAL HABITAT REQUIREMENTS: Dead or live trees infected with *Fomes*, a heartrot fungi, for cavity nest sites.

NEST: Chooses different tree species for cavity nests in different regions. In some areas, nests primarily in conifers; in others, prefers aspen, especially those infected with *Fomes*. In Colorado and Arizona, mostly nests in aspen snags or live aspen infected with *Fomes*.

FOOD: Drills rows of pits in the bark of lodgepole pine, hemlock, red and white firs, Jeffrey pine, and aspen and consumes sap and cambium. Eats ants for most of its animal food but also wood-boring larvae, moths of spruce budworm, and other insects.

REFERENCES: Baily and Neidrach 1965, Beal 1911, Bent 1939, Burleigh 1972, Crockett and Hadow 1975, Hubbard 1965, Jackman 1975, Ligon 1961, Oliver 1970, Packard 1945, Rasmussen 1941, Tatschl 1967.

Ladder-backed Woodpecker

Picoides scalaris



RANGE: Resident from southern interior California, irregularly to western Oklahoma south through Texas and Mexico to Central America.

STATUS: Locally common.

HABITAT: Occurs in wooded canyons, cottonwood groves, riparian woodlands in deserts, and dense growth of cholla cactus, creosotebush, catclaw, and other low-growing plants on borders of deserts. Also found in post oak and mesquite woodlands, and on lower slopes of mountains up to 5,500 feet.

SPECIAL HABITAT REQUIREMENTS: Trees or other structures large enough for cavity nests.

NEST: Excavates nest holes in a variety of trees (mesquite, screw bean, palo verde, hackberry, china tree, willow, cottonwood, walnut, and oak), usually 2 to 30 feet above ground. Sometimes uses saguaro, yucca stalks, telephone poles, and fence posts for nesting.

FOOD: Eats mostly insects, especially larvae of wood-boring beetles, caterpillars, and ants, but also eats fruit of various cacti.

REFERENCES: Bent 1939, Johnsgard 1979, Oberholser 1974a, Phillips et al. 1964.

Nuttall's Woodpecker

Picoides nuttallii



RANGE: Resident from northern California south, west of the deserts and the Sierra divide, to Baja California. Casual or accidental in southern Oregon, southeastern California, and Arizona.

STATUS: Common.

HABITAT: Occurs in oak woodlands, live oak forests, and chaparral, and in canyons with sycamores, alders, cottonwoods, and bay trees growing along streams lined with live oaks.

SPECIAL HABITAT REQUIREMENTS: Cavity nest sites.

NEST: Excavates cavities in dead limbs and trunks of trees, 3 to 45 feet above ground in oak, willow, sycamore, cottonwood, elder, and alder trees.

FOOD: Consumes a diet consisting of about 80 percent insects (beetles, bugs, caterpillars, and ants) which are gleaned from tree trunks and limb surfaces, or captured on the wing. Also eats wild fruits, poison oak seeds, and occasionally acorns.

REFERENCES: Beal 1911, Miller and Bock 1972, Short 1971, Terres 1980.

Downy Woodpecker

Picoides pubescens



RANGE: Breeds from western and central Alaska, northern Alberta, northern Ontario, and Newfoundland south to southern California, central Arizona, the Gulf Coast, and southern Florida. Winters throughout the breeding range, but are mostly migratory in more northern populations and occurring irregularly southward.

STATUS: Common throughout most of its range.

HABITAT: Inhabits most of the wooded parts of North America, but absent or rare in arid deserts and less common in dense forests. Favors bottomlands but also inhabits open forests and woodlots, orchards, hummocks, farmyards, and urban areas.

SPECIAL HABITAT REQUIREMENTS: Suitable cavity trees.

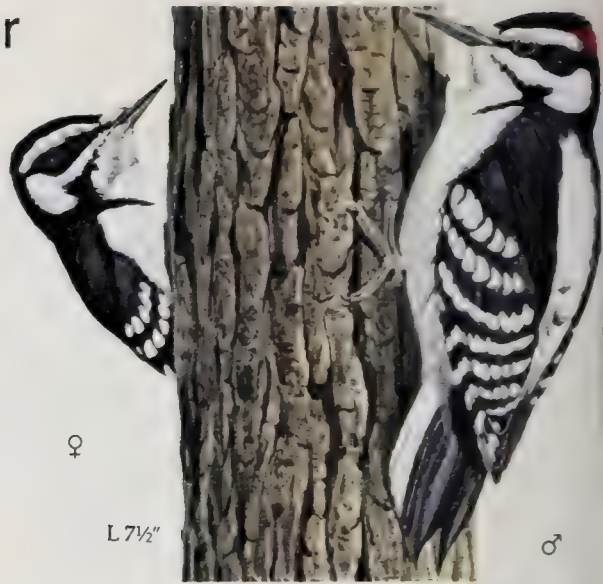
NEST: Prefers to excavate its cavity-nests near the tops of dead trees or dead limbs of live trees in fairly open tree stands. Also nests in live trees, especially if heartrot is present. Generally, excavates new cavities each year; seldom reuses old cavities or cavities of other birds. In the fall, excavates fresh holes for winter roosts.

FOOD: Consumes diet that is 75 percent animal and 25 percent vegetable material (beetles, mostly wood-boring larvae, make up a large portion of the diet). Also eats wild fruits, corn, poison sumac seeds, and mast.

REFERENCES: Beal 1911, Bent 1939, DeGraff et al. 1980, Johnsgard 1979, Kilham 1970, Lawrence 1967, Thomas 1979.

Hairy Woodpecker

Picoides villosus



RANGE: Breeds from western and central Alaska, northern Saskatchewan, and Newfoundland south throughout most of North America to Central America and the Bahamas. Winters generally throughout the breeding range, with the more northern populations partially migratory southward.

STATUS: Stable population throughout most of its range.

HABITAT: Inhabits nearly all types of forest within its range, preferring bottomlands with large mature trees. Generally more abundant at the edge of woodlands.

SPECIAL HABITAT REQUIREMENTS: Nest trees over 10 inches dbh.

NEST: Excavates cavities in snags or in live trees with decaying heartwood. Usually chooses deciduous trees such as aspens, ashes, elms, or cottonwoods.

FOOD: Consumes a diet that is about 80 percent animal food (wood-boring beetles removed from dead and diseased trees are an important source of food). Also eats other insects, fruits, corn, nuts, and cambium.

REFERENCES: Beal 1911, Bent 1939, DeGraff et al. 1980, Johnsgard 1979, Kilham 1968, Lawrence 1967, Tate and Tate 1982, Thomas et al. 1979.

Strickland's Woodpecker

Picoides stricklandi

(includes Arizona (Brown-backed) Woodpecker)



♂

L 7¼"

RANGE: Resident from southeastern Arizona and extreme southwestern New Mexico south to Mexico.

STATUS: Locally common within its limited range.

HABITAT: In the northern part of range, occurs on mountain slopes and is primarily associated with oaks, but sometimes in riparian sycamores, cottonwoods, walnuts, and willows. In the southeastern part of range also associated with pines.

SPECIAL HABITAT REQUIREMENTS: Cavity nest sites.

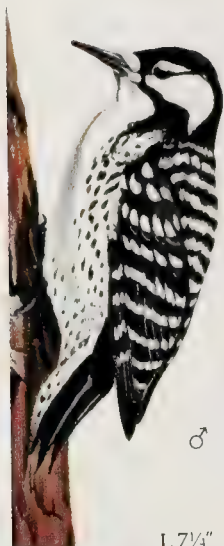
NEST: Excavates holes in dead branches of live or dead trees, primarily walnuts, oaks, maples, and sycamores.

FOOD: Feeds mainly on insects and their larvae, and some fruits and nuts.

REFERENCES: Bent 1939, Davis 1965, Terres 1980.

Red-cockaded Woodpecker

Picoides borealis



RANGE: Resident locally from eastern Oklahoma, southern Missouri, northern Arkansas, northern Mississippi, northern Alabama, northern Georgia, southeastern Virginia, and southern Maryland south to eastern Texas, the Gulf Coast, and southern Florida, and north in the Cumberland plateau through eastern Tennessee to Kentucky.

STATUS: Endangered.

HABITAT: Endemic to the yellow pine forests of the southeastern United States, where hardwoods make up less than 35 percent of the tree stand. Generally, inhabits mature forests (at least 60 years old) or younger forests where groups of mature trees are present. It is found in forests dominated by several species of pine, but probably the largest populations are found where longleaf pine is prevalent.

SPECIAL HABITAT REQUIREMENTS: Mature living pines with heartrot for nesting, and extensive pine stands for foraging.

NEST: Excavates nest holes in mature living pines infected with red heartrot. Same pair may reuse a cavity for several years. Breeds cooperatively with auxiliary or helper birds (clan) aiding a mated pair in the rearing of young. Clan size is generally two to four birds at the beginning of the breeding season.

FOOD: Prefers living pines for foraging substrate, especially larger pines. Consumes mostly insects (larvae of wood-boring insects, beetles, grubs, ants, crickets, caterpillars, scales, bark lice, and grasshoppers). Also consumes mast (primarily seeds of conifers), fruit pulp, and poison-ivy and bayberry seeds.

REFERENCES: Baker 1971, Beal 1911, Crosby 1971, Hopkins and Lynn 1971, Jackson 1971, Johnsgard 1979, Lennartz 1984, Ligon 1970, 1971b, Oberholser 1974a, Steirly 1957.

White-headed Woodpecker

Picoides albolarvatus



L 7¾"

RANGE: Resident from southern interior British Columbia, north-central Washington, and northern Idaho south through Oregon, east of the Cascades, to southern California and west-central Nevada. Casual in coastal and desert areas of southern California, but absent from the humid coastal coniferous forest.

STATUS: Local.

HABITAT: Primarily inhabits open ponderosa pine forests, but also occurs in sugar pine, Jeffrey pine, and red and white fir forests. Prefers forests with large trees and 40 to 70 percent canopy cover.

SPECIAL HABITAT REQUIREMENTS: Dead trees for cavity nests.

NEST: Usually excavates a new nest hole each year; seems to prefer dead pines. Nests in live and dead fir, oak, and aspen, with nest holes usually about 8 feet above the ground.

FOOD: Consumes primarily pine seeds, during winter and early spring (60 percent of total diet) and insects and spiders during summer.

REFERENCES: Bent 1939, Grinnel and Miller 1944, Ligon 1973, Tevis 1953, Verner and Boss 1980.



Three-toed Woodpecker

Picoides tridactylus

(formerly Northern Three-toed Woodpecker)

RANGE: Resident, often locally, from northwestern and central Alaska, northern Manitoba, northern Quebec, and Newfoundland south to western and southern Alaska, central Washington, and southern Oregon, in the Rocky Mountains to eastern Nevada, central Arizona, and south-central New Mexico, and to southwestern and central Alberta, southern Manitoba, northeastern Minnesota, central Ontario, northern New York, northern New England, and southern Quebec.

STATUS: Locally common in western coniferous forests; rare in east.

HABITAT: Primarily inhabits coniferous forests of the West, especially where fires have left large stands of dead trees. Also occasionally inhabits conifer stands in the Northeast.

SPECIAL HABITAT REQUIREMENTS: Dead trees for cavity nests.

NEST: Excavates nest cavities each year in dead trees or in dead limbs with decayed heartwood in live trees. Usually locates nest holes 5 to 12 feet above ground in pine, aspen, spruce, and cedar.

FOOD: Feeds by probing and drilling for wood-boring larvae of moths and beetles (probably one of the most important birds in combating forest insect pests in the western United States). In Colorado, consumes spruce beetles for 65 percent of its annual diet and 99 percent of its winter diet. Also eats ants, wood-boring larvae, caterpillars, fruits, mast, and cambium.

REFERENCES: Beal and McAtee 1912, Bent 1939, DeGraff et al. 1980, Jackman and Scott 1975, Johnsgard 1979, Koplín 1972, Massey and Wygant 1973, Thomas et al. 1979.

Black-backed Woodpecker

Picoides arcticus
(formerly Black-backed
Three-toed Woodpecker)



RANGE: Resident, often locally, from western and central Alaska, southern Yukon, northern Manitoba, central Labrador, and Newfoundland south to southeastern British Columbia, through the Cascade, Siskiyou, and Warner Mountains and Sierra Nevada of Washington and Oregon to central California and west-central Nevada, through Montana to northwestern Wyoming and southeastern South Dakota, and to southwestern and central Alberta, southeastern Manitoba, northern Minnesota, north-central Michigan, northern New York, and northern New England.

STATUS: Uncommon.

HABITAT: Inhabits dense coniferous forests, especially in burned, swampy, cutover, or beetle-killed forests where dead trees are numerous.

SPECIAL HABITAT REQUIREMENTS: Dead or live trees with dead heartwood for nesting and feeding sites.

NEST: Usually excavates its cavities in snags or live trees with dead heartwood, especially in areas that have been burned or logged. Mostly nests in spruce, balsam fir, pines, or Douglas-fir, but also in maple, birch, cedar, and utility poles. Locates nest cavity usually less than 15 feet above the ground.

FOOD: Flakes off bark of dead conifers to get at larvae of destructive wood-boring beetles, which make up about 75 percent of its food. Also eats weevils and other beetles, spiders, and ants, along with some wild fruit, mast, and cambium.

REFERENCES: Beal and McAtee 1912, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Thomas et al. 1979.

Northern Flicker

Colaptes auratus
(formerly Common Flicker)



Yellow-shafted

Red-shafted

L 10½"

RANGE: Breeds from central Alaska, northern Manitoba, north-central Quebec, and Newfoundland south throughout most of North America and northwestern Mexico. Winters from southern Canada south through the breeding range.

STATUS: Common.

HABITAT: Commonly found near large trees in open woodlands, fields, meadows, and deserts throughout North America. In winter, occasionally seeks shelter in coniferous forests or in swamps.

SPECIAL HABITAT REQUIREMENTS: Cavity nest sites.

NEST: Prefers to nest near the top of broken-off stubs of dead trees in open country or in sparsely wooded parklike suburban areas. Also nests in and around openings in extensive forested areas. Excavates nests in dead or live trees of many species, including aspen, cottonwood, oak, willow, sycamore, pine, and juniper.

FOOD: Searches for food, much of the time, on the ground. Consumes a diet that is about 60 percent animal food; of this, nearly 75 percent is ants. (Some flicker stomachs have contained over 2,000 ants.) The diet also includes other insects, weed seeds, cultivated grain, and the fruits of shrubs and trees.

REFERENCES: Bailey and Niedrach 1965, Beal 1911, Conner et al. 1975, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Lawrence 1967, Thomas et al. 1979.

Pileated Woodpecker

Dryocopus pileatus

L 15"

♂



RANGE: Resident from southern and eastern British Columbia, southwestern Mackenzie, central Manitoba, New Brunswick, and Nova Scotia south through Alberta, Washington, south-central Idaho, western Montana, and Oregon to northern California, west to eastern Dakotas, Missouri, and Oklahoma and south to east-central Texas, the Gulf Coast, and southern Florida.

STATUS: Locally common but has become less common in areas where extensive agricultural or logging practices have eliminated large tracts of old-growth forests.

HABITAT: Generally limited to mature coniferous, deciduous, and mixed forests with large, dead trees. Prefers woodlands near water.

SPECIAL HABITAT REQUIREMENTS: Large dead trees for nesting and feeding.

NEST: Usually excavates nest holes in dead tree trunks or dead limbs of living trees. Generally requires trees greater than 15 inches dbh for nest and roost cavities and generally uses ponderosa pine snags greater than 20 inches dbh. Nests in a variety of tree species, including beech, cottonwood, yellow-poplar, birch, oak, hickory, maple, hemlock, pine, ash, elm, basswood, and aspen.

FOOD: Consumes a diet that is about 70 percent insects, with ants, especially carpenter ants and wood-boring beetles, predominating. Also consumes other insects, some wild fruits, mast, and seeds of sumac.

REFERENCES: Beal 1911, Bull and Meslow 1977, Conner et al. 1975, DeGraff et al. 1980, Forbush and May 1955, Hoyt 1957, Johnsgard 1979.

Ivory-billed Woodpecker

Campephilus principalis

L 18"



RANGE: Formerly resident from eastern Texas, southeastern Oklahoma, northeastern Arkansas, southeastern Missouri, southern Illinois, southern Indiana, Kentucky, and southeastern North Carolina south to the Gulf Coast, southern Florida, and Cuba.

STATUS: Endangered; may be extinct or nearly so.

HABITAT: Inhabits old-age forests of bottomlands and swamps with dead and dying trees that provide a food source and nest sites. Most birds live in virgin or primitive tree stands, but virgin forests may not be essential as long as there are large numbers of recently dead trees to supply wood-boring grubs and large nesting trees.

SPECIAL HABITAT REQUIREMENTS: Continual supply of dead and dying trees.

NEST: Excavates a new hole each nesting season, seldom in the same tree, in almost all tree species occurring within its range, and in trunks of living and dead trees.

FOOD: Consumes a diet that is about one-third wood-boring larvae. Most abundant in areas where recently dead and dying trees are numerous because of flooding, fire, insect attacks, or storms; stays as long as abundant wood-boring larvae are present. (Wood-boring larvae begin to decline after trees have been dead 2 or 3 years.) Also eats other insects and fruits.

REFERENCES: Beal 1911, Cottam and Knappen 1939, Dennis 1967, Forbush and May 1955, Greenway 1958, Mackenzie 1977, Oberholser 1938, Pearson 1936, Tanner 1966, USDI Fish and Wildlife Service 1980.

Northern Beardless-Tyrannulet

Camptostoma imberbe
(formerly Beardless Flycatcher)



L 3½"

RANGE: Breeds from southeastern Arizona, extreme southwestern New Mexico in Guadalupe Canyon, and Kenedy County in Texas south to Costa Rica. Winters in Mexico and Central America, casually to southern Arizona.

STATUS: Fairly common to rare.

HABITAT: In Arizona, occurs in cottonwoods, dense mesquite thickets, and in sycamore-live oak-mesquite associations. Along the lower Rio Grande Valley in Texas, inhabits mesquite woodlands, cottonwoods, willows, elms, and great luecaenas.

NEST: Typically nests far out on a horizontal limb of a bush or tree up to 50 feet high, but usually near the ground. Usually nests along the edge of a grove, or among scattered trees in flat, sandy lowlands. Locates nest in a clump of mistletoe or sometimes between the bases of stems of palmetto fans.

FOOD: Perches on the top branch of a tree or in lower branches to flycatch and glean scale insects, caterpillars, and ants. Occasionally eats small berries and seeds.

REFERENCES: Bent 1942, Harrison 1979, Oberholser 1974a, Phillips et al. 1964, Terres 1980.

Olive-sided Flycatcher

Contopus borealis



L 6¼"

RANGE: Breeds from western and central Alaska and central Yukon to northern Ontario, south-central Quebec, and southern Labrador south to southern California across to western Texas, and east of the Rocky Mountains, to central Saskatchewan, northern Wisconsin, northeastern Ohio, and Massachusetts; also locally in the Appalachians to western North Carolina. Winters in South America and, casually, in southern California.

STATUS: Local to fairly common.

HABITAT: Inhabits montane and northern coniferous forests up to 10,000 feet in elevation, especially in burned-over areas with tall standing dead trees. Prefers forests of tall spruces, firs, balsams, and pines; groves of eucalyptus and Monterey cypress; taiga; subalpine coniferous forests; mixed woodlands near edges and clearings; and wooded streams and borders of northern bogs and muskegs. Prefers stands with a low percentage of canopy cover.

SPECIAL HABITAT REQUIREMENTS: Tall, exposed perches such as snags or high, conspicuous dead branches.

NEST: Usually hides nests in a cluster of needles and twigs on a horizontal branch of a conifer, well away from the trunk, usually between 15 and 50 feet above the ground.

FOOD: Typically perches in tree tops and on high exposed limbs to hawk flying insects.

REFERENCES: Bent 1942, Beal 1912, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Terres 1980.

Greater Pewee

Contopus pertinax
(formerly Coues' Flycatcher)



L 6"

RANGE: Breeds from central Arizona and southwestern New Mexico south to Central America. Winters in Mexico and Central America, casually north to southern Arizona.

STATUS: Fairly common.

HABITAT: Occurs in mountains up to 10,000 feet near the Mexico border, where it inhabits pine and pine-oak forests with an undergrowth of bushes. Also occurs in sycamore groves along mountain canyons.

SPECIAL HABITAT REQUIREMENTS: Tall trees for feeding perches and for nesting.

NEST: Locates nest on a horizontal fork 10 to 40 feet above the ground in a pine, sycamore, spruce, maple, oak, or other tall tree. Vigorously defends nest against jays, hawks, squirrels, and snakes.

FOOD: Hawks insects from a perch high up in a tall tree. (There are no detailed reports of its food habits.)

REFERENCES: Bent 1942, Harrison 1979, Phillips et al. 1964, Terres 1980.

Western Wood-Pewee

Contopus sordidulus



L 5¼"

RANGE: Breeds from east-central Alaska, southern Yukon, and southern Mackenzie to northwestern Minnesota, south to Mexico, and east to western South Dakota, western Kansas, and western Texas. Winters in South America.

STATUS: Common.

HABITAT: Occurs in a variety of habitats including open deciduous and coniferous montane forests, pine-oak woodlands, floodplain forests, and wooded canyons. Found from sea level to the tops of coastal ranges, in cultivated stream valleys, in deciduous trees along borders of lakes and streams, in cities and towns, and in open, mature pine forests. It is generally adapted to drier environments than the eastern wood-pewee, and uses areas dominated by conifers.

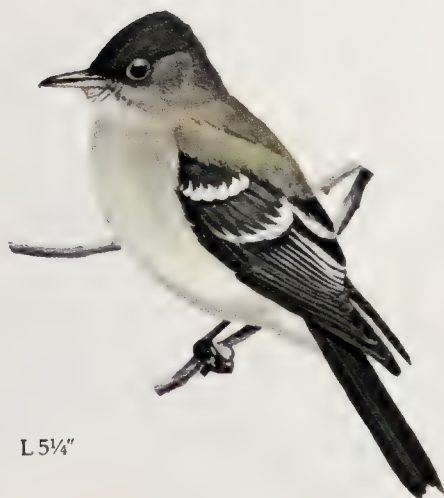
NEST: Locates nest on a horizontal limb or fork, dead or live, in a large variety of trees, usually deciduous, generally 15 to 40 feet above the ground.

FOOD: Catches most of its food by hawking from a perch such as a dead branch. Eats insects, spiders, and a few wild berries.

REFERENCES: Beal 1912, Harrison 1979, Johnsgard 1979, Terres 1980.

Eastern Wood-Pewee

Contopus virens



L 5¼"

RANGE: Breeds from southeastern Saskatchewan to southern Quebec and New Brunswick, south to Texas, the Gulf Coast, and central Florida, and west to the eastern Dakotas, central Oklahoma, and south-central Texas. Winters in South America.

STATUS: Common.

HABITAT: Generally associated with deciduous forests; prefers woodlands with a relatively open understory but will use areas with a dense understory if the canopy above is incomplete or sparse. Also inhabits mixed forests, bottomlands, uplands, woodlots, orchards, parks, roadsides, and suburban areas planted to trees. Occurs in floodplain and river-bluff forests at the western edge of its range. Appears to be strongly associated with oaks, and throughout its range probably requires a predominance of hardwoods.

NEST: Locates nest on a horizontal limb usually well out from the trunk, 9 to 65 feet above the ground, often on a dead limb in a living tree. Camouflages nest with spiderwebs and lichens.

FOOD: Prefers to flycatch in a shady spot from mid to low level of the tree canopy. Eats insects, spiders, and millipedes, and also a few berries and seeds.

REFERENCES: Beal 1912, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979.

Yellow-bellied Flycatcher

Empidonax flaviventris



L 4½"

RANGE: Breeds from northern British Columbia and west-central and southern Mackenzie to southern Labrador and Newfoundland south to central Alberta, northern North Dakota, and northern Minnesota, across to southern Ontario, northeastern Pennsylvania, and Nova Scotia. Winters from Mexico to South America.

STATUS: Common.

HABITAT: Prefers predominantly coniferous forests of spruce and fir, frequenting low, swampy thickets bordering ponds and streams, spruce, cedar, tamarack and sphagnum bogs, spruce and alder swamps, wet mossy glades, and cool moist mountainsides.

SPECIAL HABITAT REQUIREMENTS: Low, wet areas within coniferous forest.

NEST: Nests on or near the ground, sometimes at the base of a tree or in a cavity formed by upturned roots, but more often beside a hummock or mound and well-hidden in sphagnum moss or other vegetation. May also nest in a damp, mossy crevice of rocks, but always in a quiet, concealed site.

FOOD: Perches and feeds close to the ground, mainly on insects, which form 97 percent of the diet; occasionally eats a few berries.

REFERENCES: Beal 1912, Bent 1942, DeGraff et al. 1980, Forbush and May 1955, Terres 1980.

Acadian Flycatcher

Empidonax virescens



RANGE: Breeds from southeastern South Dakota, northern Iowa, and extreme southeastern Minnesota to southern New York, Vermont, and Massachusetts, south to central and southern Texas, the Gulf Coast, and central Florida. Winters in Central and South America.

STATUS: Common

HABITAT: Inhabits the lowest tree canopy and understory layers of shady, humid riverbottom forests and wooded swamps. Prefers damp, lowland forests with an understory and uplands with wooded ravines near streams. Favors beech forests in the Northeast.

SPECIAL HABITAT REQUIREMENTS: Mature, extensive deciduous forests with tall trees, a closed canopy, and open spaces in understory for feeding.

NEST: Nests on a fork of a horizontal branch well away from the main trunk, usually 10 to 20 feet above the ground, often along a stream and sometimes over water. Prefers open space below the nest to approach the nest easily. Favors lower branches of beech, dogwood, and witch-hazel, but also nests in oak, hickory, maple, basswood, and cherry. Occasionally is parasitized by brown-headed cowbirds.

FOOD: Eats mostly insects; also eats some spiders and millipedes, and occasionally a few seeds and berries.

REFERENCES: Beal 1912, Bent 1942, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Mumford 1964.

Alder Flycatcher

Empidonax alnorum

WILLOW
AND ALDER
FLYCATCHERS



RANGE: Breeds from central Alaska and central Yukon to central and eastern Quebec, southern Labrador and southern Newfoundland, south to south-central British Columbia and southern Alberta, across to south-central Minnesota, eastern Pennsylvania, and Connecticut; also in the Appalachians south to western North Carolina. Winters in South America.

STATUS: Common.

HABITAT: Typically inhabits northern alder swamps, where it occupies a variety of habitats, including thickets of aspen parkland. Usually found near water in dense, low, damp thickets of alders, willows, sumacs, viburnum, elderberries, and red-osier dogwood bordering bogs, swamps, marshes, and along the banks of small streams and shores of ponds.

SPECIAL HABITAT REQUIREMENTS: Forest openings and edges with dense, low shrubs.

NEST: Nests in low trees or shrubs including dogwood, blackberry, hawthorn, viburnum, willow, spiraea, or alder, 1 to 6 feet above the ground, in an upright fork or saddled on a branch.

FOOD: Catches at least 65 species of beetles as well as other flying insects, spiders, and millipedes; eats some fruits.

REFERENCES: Bent 1942, DeGraff et al. 1980, Eckert in Farrand 1983b, Mousley 1931, Stein 1958, Terres 1980.

Willow Flycatcher

Empidonax traillii

RANGE: Breeds from central British Columbia and southern Alberta east to southern Wisconsin, southern Quebec, central Maine, and Nova Scotia south to southern California, western and central Texas, Arkansas, northern Georgia, and central and eastern Virginia. Winters in Mexico and Central America.

STATUS: Common; population is generally stable or increasing throughout its range.

HABITAT: Occurs in a variety of habitats ranging from brushy fields to willows, thickets along streams, prairie woodlots, shrubby swales, and open woodland edges. Prefers edge habitats that include thickets or groves of small trees and shrubs surrounded by grasslands, as well as the edges of gallery forests along rivers or streams. In areas where its range overlaps that of the alder flycatcher, prefers drier, smaller, more open shrubby habitat.

SPECIAL HABITAT REQUIREMENTS: Fairly open and well-spaced shrubby habitats.

NEST: Nests usually in horizontal forks or upright crotches of shrubs or small trees, usually between 3 to 25 feet above the ground, averaging about 4 to 6 feet. Commonly nests in dogwood, hawthorn, willow, buttonbush, elder, viburnum, and blackberry. Places nest at the outer edge of a shrub or thicket, so it can be easily approached.

FOOD: Eats flying insects.

REFERENCES: Bent 1942, DeGraff et al. 1980, Eckert in Farrand 1983b, Holcomb 1972, Johnsgard 1979, King 1955, Stein 1958, Tate and Tate 1982, Walkinshaw 1966.

Least Flycatcher

Empidonax minimus



RANGE: Breeds from southern Yukon and west-central and southern Mackenzie to southern Quebec and New Brunswick, south to southern British Columbia and central Montana, across to southwestern Missouri, northern Ohio, and central New Jersey; in the Appalachians to northwestern Georgia. Winters in Mexico and Central America; also casually in southern California, southern Texas, and Florida.

STATUS: Common; population is declining slightly in parts of its range.

HABITAT: Associated with open deciduous forests, where it occurs along forest edges, burns, and clearings, floodplain forests, open shrublands, wooded margins of lakes and roads, orchards, shelterbelts, overgrown pastures, urban parks, and gardens.

SPECIAL HABITAT REQUIREMENTS: Intermediate openness in the understory of open deciduous woodlands, and some edge habitat for nesting and feeding.

NEST: Nests in upright crotch or on horizontal fork of deciduous or coniferous trees, usually saplings or small trees, including birch, red pine, cedar, apple, dogwood, oak, sugar maple, willow, and alder. Tends to nest at the edge of a clearing 10 to 20 feet above the ground, but will nest from 2 to 60 feet.

FOOD: Feeds mainly on flying insects, most of which are caught on the wing, but some are gleaned from vegetation. Also takes a few fruits and seeds.

REFERENCES: Beal 1912, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, de Kirilene 1948, Tate and Tate 1982.

Hammond's Flycatcher

Empidonax hammondii



RANGE: Breeds from east-central Alaska, southern Yukon, and southwestern Alberta to northwestern Wyoming, south to east-central California, central Utah, northeastern Arizona, and north-central New Mexico. Winters in southeastern Arizona, Mexico, and Central America, casually in southern California.

STATUS: Common.

HABITAT: Inhabits tall, moist, closed-canopy montane conifer forests, sometimes with a deciduous understory. In Colorado, occurs from 7,500 to 11,000 feet in conifer-aspen woodlands; in California, in mature forests of medium to high canopy coverage from ponderosa pine up to lodgepole pine forests. In the far North, prefers deciduous forests.

SPECIAL HABITAT REQUIREMENTS: Nest sites that are cool and well shaded.

NEST: Nests in a fork of a small tree or on a horizontal branch of a large conifer or deciduous tree, usually 25 to 40 feet above the ground. Uses birch, maple, ponderosa pine, western larch, and Douglas-fir for nesting.

FOOD: Prefers to forage from the middle portions of tall conifers and aspens on flying insects.

REFERENCES: Bailey in Farrand 1983b, Beaver and Baldwin 1975, Davis 1954, Terres 1980, Verner and Boss 1980.

Dusky Flycatcher

Empidonax oberholseri



L 4¾"

RANGE: Breeds from southwestern Yukon, southern Alberta, southwestern Saskatchewan, and western South Dakota south to southern California, southern Nevada, central Arizona, and central and northeastern New Mexico. Winters in southern Arizona and Mexico; casual in southern California.

STATUS: Common.

HABITAT: Prefers shrubby sites or low- to intermediate-density forests with substantial shrub understory; generally avoids forests with a high percentage of canopy cover. Occurs in a variety of habitats, from montane chaparral to moderately dense lodgepole pine forest, including many montane conifer types and aspen; especially favors mixed woodlands or edge of small conifers and brush. In general, prefers drier, more open or patchier forests than Hammond's flycatcher.

NEST: Builds nests on upright or pendant twigs or in crotches of low shrubs or trees in relatively dry sites. Usually nests 3 to 8 feet, but up to 40 feet, above the ground in willow, alder, aspen, and other trees and shrubs.

FOOD: Forages low over shrubby vegetation for flying insects.

REFERENCES: Bailey in Farrand 1983b, Harrison 1979, Johnsgard 1979, Verner and Boss 1980.

Gray Flycatcher

Empidonax wrightii



RANGE: Breeds from south-central Washington and south-central Idaho to central Colorado, south to south-central California, central Arizona, and south-central New Mexico. Winters in central Arizona and Mexico, rarely in southern California.

STATUS: Fairly common.

HABITAT: Associated with arid woodland and brushy areas, where it inhabits tall sagebrush plains, pinyon-juniper woodlands, and arid, very open pine woods. During migration and in winter it occurs in arid scrub, riparian, and mesquite woodlands.

NEST: Nests in a crotch of a thornbush, juniper, or sagebrush, 2 to 5 feet above the ground, sometimes in loose colonies.

FOOD: Does most of its foraging in the spaces between bushes, and often flies to snatch insects from the ground. Catches insects from the size of tiny beetles to butterflies.

REFERENCES: Bailey in Farrand 1983b, Phillips et al. 1964, Russell and Woodbury 1941, Terres 1980.

Western Flycatcher

Empidonax difficilis



RANGE: Breeds from southeastern Alaska, northwestern and central British Columbia, and southwestern Alberta to western South Dakota, south along the coast and mountains to southwestern California, central Nevada, central and southeastern Arizona, and western Texas. Winters in Mexico.

STATUS: Common.

HABITAT: Found in a variety of wooded habitats; prefers moist, shaded forests, either coastal or lower montane, or higher in the Rockies and Great Basin ranges. Also inhabits hollows, canyon bottoms, riparian woodlands, and deciduous, coniferous, and mixed forests.

SPECIAL HABITAT REQUIREMENTS: A sheltered nest site, possibly near a water source such as a stream, spring, or seep.

NEST: May use a variety of sites for nesting; these include rock ledges or crevices of canyon walls, often concealed by ferns or clumps of mosses; crotch or tree limb projecting from the main trunk; behind flaps of loose bark; tree cavities; or old buildings. Nest height ranges from ground level up to 30 feet.

FOOD: Commonly forages within shaded forests for insects and spiders. Also eats a few seeds.

REFERENCES: Bailey in Farrand 1983b, Beal 1912, Beaver and Baldwin 1975 Davis et al. 1963, Johnsgard 1979, Verner and Boss 1980.

Buff-breasted Flycatcher

Empidonax fulvifrons



L 4''

RANGE: Breeds very locally from the Huachuca and Chiricahua Mountains of east-central and southeastern Arizona through Mexico. Winters in Mexico.

STATUS: Rare and local.

HABITAT: Prefers open stands of pines and riparian trees, but also occurs in mixed pine and oak woods with shrubby undergrowth and on steep canyon slopes, from 5,000 to 8,500 feet. Favors open trees with bare, weedy, or grassy places.

SPECIAL HABITAT REQUIREMENTS: Forest openings.

NEST: Places nest on a branch 9 to 45 feet above the ground, often sheltered by an overhanging stub of a branch. Builds nests in pines, oaks, and sycamores.

FOOD: Often forages for insects from the low scrubby understory or close to the trunk, low or at midlevel in pines.

REFERENCES: Bent 1942, Cottam and Knappen 1939, Phillips et al. 1964, Terres 1980, Terrill in Farrand 1983b.

Black Phoebe

Sayornis nigricans



RANGE: Resident from northwestern California, southern Nevada, southwestern Utah, south-central Colorado, and western and west-central Texas south to South America. (Partially migratory, northern populations wander after the breeding season).

STATUS: Common.

HABITAT: Occurs in a variety of open and wooded habitats, usually near water, especially in drier regions. Found in the vicinity of streams, canals, lake margins, reservoirs, or other riparian sites flanked by grasslands, scattered trees, open woodlands or farmland. During migration and in winter, found at almost any source of water.

SPECIAL HABITAT REQUIREMENTS: Vertical surface for nesting that is protected from rain, near a mud source, and preferably near water.

NEST: Builds a mud nest commonly under bridges, in culverts and wells, under the eaves of buildings as well as on the vertical surfaces of cliffs, rimrocks, steep creek banks, and caverns. May use the same nest site year after year.

FOOD: Catches insects over grassy fields and open water, or gleans them from plant foliage. Also eats some fruits of buckthorn.

REFERENCES: Ohlendorf 1976, Phillips et al. 1964, Terres 1980.

Eastern Phoebe

Sayornis phoebe



L 5 3/4"

RANGE: Breeds from northeastern British Columbia and west-central and southern Mackenzie to southwestern Quebec and central New Brunswick, south to southern Alberta, southwestern South Dakota, central New Mexico, and central and northeastern Texas across to northern Georgia and North Carolina. Winters from central Texas, the Gulf States, and Virginia south to Mexico and southern Florida; casually from Oklahoma, southern Ontario, and New England.

STATUS: Common.

HABITAT: Generally occurs near fresh running water in partially wooded habitats; frequents woodland edges, wooded ravines and cliffs, farms, and suburban areas where natural or artificial ledges are available for nesting.

SPECIAL HABITAT REQUIREMENTS: Cliffs or ledges at stream-side clearings, or structures at forest openings for nesting. Perches 5 to 15 feet high for feeding.

NEST: Nests on a ledge, usually sheltered above by an overhang, on natural or artificial structures, and generally near lakes or streams. May nest under bridges, culverts, or eaves of buildings, on cliffs, rock bluffs, or in ravines. Frequently uses nests from previous years, but is very adaptable in its nesting habits. Frequently the victim of cowbird parasitism.

FOOD: In late winter and early spring, subsists mainly on seeds and wild berries; at other times, feeds on insects, usually hawking them from a perch.

REFERENCES: Beal 1912, DeGraff et al. 1980, Forbush and May 1955, Hespenheide 1971, Johnsgard 1979, Tate and Tate 1982, Weeks 1979.

Say's Phoebe

Sayornis saya

L 6¼"



RANGE: Breeds from western and northern Alaska, northern Yukon, northwestern and central Mackenzie, and central Alberta to southwestern Manitoba, south between coastal ranges and central prairie states to Mexico. Winters from northern California, Arizona, central New Mexico, and central Texas south to Mexico.

STATUS: Common.

HABITAT: Inhabits open arid regions, occurring in dry, barren foothills, sagebrush plains, scrubby pine-oak-juniper woodlands, bluffs and cliffs of the badlands, grasslands, canyons, and open areas near buildings. Unlike the eastern phoebe, it is independent of surface water.

NEST: Prefers to nest in holes, crevices, on ledges, and on other protected horizontal surfaces of cliffs, rimrocks, steep creek banks, and caverns. Frequently nests in abandoned mine shafts, buildings, and under bridges. Also uses old nests of cliff swallows, barn swallows, and black phoebes; often uses the same nest in subsequent years or for successive clutches.

FOOD: Eats mostly insects (primarily grasshoppers) and some berries.

REFERENCES: Beal 1912, Bent 1942, Johnsgard 1979, Ohlendorf 1976, Terres 1980.

Vermilion Flycatcher

Pyrocephalus rubinus



L 5"

RANGE: Breeds from southern California, southern Nevada, central Arizona, central New Mexico, and western Oklahoma south to South America. Winters from southern California and southern Nevada to the Gulf Coast, east to south-central Florida, and south to Central America.

STATUS: Common.

HABITAT: Found in the arid Southwest, occurring almost exclusively near water. Favor wooded groves of cottonwood, willow, oak, mesquite, and sycamore bordering rivers, especially near open, brushy, grassy, or agricultural fields. Also occurs in widely spaced junipers and oaks, and in dry washes on the plains.

NEST: Builds nest on a small, horizontal forked branch usually 8 to 20 feet, but sometimes 40 to 50 feet, above the ground, and usually near a stream or other source of water. Nests in willow, sycamore, mesquite, cottonwood, oak, paloverde, hackberry, and other trees and bushes.

FOOD: Forages from a conspicuous perch, often only a few feet above the ground or water, for insects such as bees, grasshoppers, and small beetles.

REFERENCES: Bent 1942, Harrison 1979, Johnsgard 1979, Taylor and Hanson 1970, Terres 1980, Terrill in Farrand 1983b.

Dusky-capped Flycatcher

Myiarchus tuberculifer
(formerly Olivaceous Flycatcher)



L 5¾"

RANGE: Breeds in southeastern Arizona and southwestern New Mexico; also in Central and South America. Winters from Mexico to South America.

STATUS: Fairly common.

HABITAT: Generally found below 6,000 feet but does occur up to 7,500 feet in montane pine-oak woodlands. Prefers dense scrub oak thickets on hillsides but also occurs along canyon streams where trees grow thick enough to provide deep shade.

SPECIAL HABITAT REQUIREMENTS: Natural cavities or old woodpecker holes in trees for nesting.

NEST: Builds nests in natural cavities in trees and stumps or in old woodpecker holes, 4 to 50 feet above the ground, in oaks, sycamores, or ashes.

FOOD: Eats small insects.

REFERENCES: Bent 1942, Cottam and Knappen 1939, Harrison 1979, Phillips et al. 1964, Terres 1980.

Ash-throated Flycatcher

Myiarchus cinerascens



L 6½"

RANGE: Breeds from northwestern Oregon and eastern Washington to Colorado and western Kansas, south to Mexico. Winters from southern California and central Arizona south to Central America.

STATUS: Common.

HABITAT: Inhabits mesquite and cactus deserts, rocky mesas, shrubby canyons, oak groves on hillsides, mesquite thickets along creek bottoms, open pinyon-juniper woodlands, and open groves of sycamore, oak, willow, or cottonwood along stream courses. Stands with a low percentage of canopy cover are preferred. Occurs from sea level to 9,000 feet in California, but is most frequently found at lower elevations.

SPECIAL HABITAT REQUIREMENTS: Natural tree cavities or old woodpecker holes for nesting.

NEST: Uses a variety of cavities for nesting; natural cavities or knot holes in trees and stumps of mesquite, ash, oak, sycamore, juniper or cottonwood, or old woodpecker holes. May also nest behind loose pieces of bark, in abandoned nests of cactus wrens, in cavities in saguaro, in artificial structures, or in stalks of yucca or agave. Usually nests less than 20 feet above the ground.

FOOD: Forages over low shrubs, hawking insects and spiders. Also eats a few fruits and seeds.

REFERENCES: Beal 1912, Bent 1942, Johnsgard 1979, Terres 1980.

Great Crested Flycatcher

Myiarchus crinitus



L 7"

RANGE: Breeds from east-central Alberta and central and southeastern Saskatchewan to south-western Quebec and central New Brunswick, south to central and southeastern Texas, the Gulf Coast, and Florida, and west to the eastern Dakotas, western Kansas, and west-central Oklahoma. Winters in central and southern Florida and from Mexico to South America.

STATUS: Common.

HABITAT: Prefers fairly extensive hardwood forests but is commonly found in old orchards and woodlots in farming country, clearings in mixed and deciduous forests, and wooded residential areas. Prefers forests with mature trees and fairly open canopies but will also use second-growth woodlands.

SPECIAL HABITAT REQUIREMENTS: Cavities in middle-aged to mature trees, preferably in deciduous forests.

NEST: Nests in woodpecker holes or in natural cavities in live or dead trees, usually 10 to 20 feet, but sometimes from 3 to 75 feet, above the ground. May also use artificial structures such as bird houses and other hollows, with little preference shown for the shape of the opening or the cavity expanse.

FOOD: Forages in the forest canopy and gleans a variety of insects and spiders from crevices in the bark of trees; also eats some fruits.

REFERENCES: Beal 1912, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Mousley 1934a.

Brown-crested Flycatcher

Myiarchus tyrannulus

(formerly Wied's Crested Flycatcher)



L 7¼"

RANGE: Breeds from southeastern California, extreme southern Nevada, southwestern Utah, Arizona, and southwestern New Mexico south to Central America. Winters in Mexico and Central America; rarely in southern Florida.

STATUS: Fairly common.

HABITAT: Inhabits saguaro deserts, riparian deciduous woodlands, and shade trees in urban areas. In Texas, occurs in open woodlands of mesquite, hackberry, and ash; in Arizona, frequents cottonwood, willow, and sycamore woodlands.

SPECIAL HABITAT REQUIREMENTS: Natural tree cavities or abandoned woodpecker holes for nesting.

NEST: Builds nest in abandoned woodpecker holes in saguaro or in cavities in cottonwoods, sycamores, mesquite, or old fence posts 5 to 30 feet above the ground. Sometimes nests in bird houses.

FOOD: Probably eats beetles, other flying insects, and some wild berries and fruits; has been observed eating hummingbirds.

REFERENCES: Bent 1942, Gambona 1977, Oberholser 1974a, Phillips et al. 1964.

Great Kiskadee

Pitangus sulphuratus
(formerly Kiskadee Flycatcher)



L 9"

RANGE: Resident in southern Texas north to Webb County and the Corpus Christi area and south to South America.

STATUS: Locally common.

HABITAT: Found in the lower Rio Grande Valley, along river beds, streams, ponds, and stagnant watercourses among large trees of mesquite, huisache, palm, baldcypress, and willow, with thick undergrowth of shrubs and small trees. Also inhabits groves and orchards and is found in trees around ranches and urban areas.

NEST: Builds nest in trees or tall shrubs, usually 10 to 20 feet, but up to 30 feet, above ground in brushy sites, low woods, along streams, marshes, or lagoons, or in cultivated areas. May nest in mesquite, palm, pine, acacia, or in a thorny bush.

FOOD: Fishes for minnows, tiny fishes, and tadpoles by perching on a low branch overhanging water and diving, barely breaking the water's surface. Also eats water insects, flying insects, and some fruits and berries, especially in winter.

REFERENCES: Bent 1942, Oberholser 1974a, Terres 1980.

Sulphur-bellied Flycatcher

Myiodynastes luteiventris



L 6¾"

RANGE: Breeds from southeastern Arizona to Central America. Winters in South America.

STATUS: Fairly common.

HABITAT: Inhabits riparian mountain canyons, from 5,000 to 7,500 feet in elevation, where sycamore, oak, walnut, Arizona cypress, and pine are common.

SPECIAL HABITAT REQUIREMENTS: Natural cavities in trees or abandoned northern flicker holes.

NEST: Usually builds nest in a natural cavity, typically a knothole where a large branch has broken off and a cavity has rotted out, 20 to 50 feet above the ground in living sycamores. Occasionally nests in an old flicker hole or a nest box placed high in a tree. Constructs nest on top of a loose platform built inside the cavity.

FOOD: Eats a variety of insects and spiders; also a few small fruits and berries.

REFERENCES: Bent 1942, Cottam and Knappen 1939, Ligon 1971a, Phillips et al. 1964.

Tropical Kingbird

Tyrannus melancholicus



L 7"

RANGE: Breeds from southeastern Arizona to South America. Winters in Mexico south to South America.

STATUS: Uncommon and local.

HABITAT: Inhabits groves of tall trees, especially cottonwoods, next to ponds or flowing streams at low elevations. Frequently occurs along with both the western and Cassin's kingbirds.

NEST AND FOOD: Has nesting and food habits similar to those of western and Cassin's kingbirds, with which it closely associates.

REFERENCES: Kaufman in Farrand 1983b, Terres 1980.

Couch's Kingbird

Tyrannus couchii

(split from Tropical Kingbird)

RANGE: Resident from southern Texas north to Webb and Kenedy Counties, south to Central America.

STATUS: Fairly common.

HABITAT: Frequents the borders of woods, chaparral, and trees along lakes, ponds, rivers, and stagnant watercourses, where it inhabits groves of mesquite, ebony blackbead, retaima, granjena, persimmon, and thorny bushes. It also frequents urban areas.

NEST: Nests on a branch or in a fork of a tree 8 to 20 feet above the ground in woodlands and brush, along marshy or brushy margins of lakes or rivers, and in cultivated areas.

FOOD: Frequently perches on tall trees to hawk insects.

REFERENCES: Bent 1942, Harrison 1979, Kaufman in Farrand 1983b, Oberholser 1974a.

Cassin's Kingbird

Tyrannus vociferans



L 7''

RANGE: Breeds from central California, southern Utah, Colorado, and southeastern Montana south to Mexico, and east to western Texas. Winters in Mexico and Central America; irregularly from central California.

STATUS: Fairly common.

HABITAT: Occurs in open country such as plains and semideserts, in a variety of habitats from desert riparian areas up to 7,500 feet and in open woodlands in southwestern mountains. Inhabits pinyon-yucca, pinyon-juniper, pine-oak, and ponderosa pine woodlands, canyons of sycamores, and in California, open valley woodlands and grasslands of the foothills among scattered oaks, cottonwoods, and sycamores.

SPECIAL HABITAT REQUIREMENTS: Tall trees for nesting.

NEST: Usually nests in fairly tall trees such as pine, oak, cottonwood, walnut, hackberry, or sycamore. Places nest near the end of a horizontal limb 8 to 40 feet, but up to 100 feet, above the ground. Also places nests in bushes and on posts.

FOOD: Primarily eats insects, but also spiders and fleshy fruits.

REFERENCES: Beal 1912, Bent 1942, Hespenheide 1964, Johnsgard 1979, Ohlendorf 1974, Terres 1980, Terrill in Farrand 1983b.

Thick-billed Kingbird

Tyrannus crassirostris



L 7¼"

RANGE: Breeds from the Patagonia and Guadalupe mountains in southeastern Arizona, and Guadalupe Canyon in extreme southwestern New Mexico south to Mexico. Winters in Mexico.

STATUS: Rare; first discovered in the United States in 1958, the range of this Mexican species has expanded northward since the middle of the 20th century.

HABITAT: Occurs near sycamore trees in streamside habitats dominated by cottonwood, willow, and mesquite.

NEST: In the United States, nests in streamside sycamores 50 to 60 feet above the ground.

FOOD: Presumably eats insects; commonly flies great distances between perches.

REFERENCES: Levy 1959 , Oberholser 1974a, Phillips et al. 1964, Terres 1980, Terrill in Farrand 1983b.

Western Kingbird

Tyrannus verticalis



L 7"

RANGE: Breeds from southern interior British Columbia to southern Manitoba and western Minnesota south to Baja California, Mexico, and southern and south-central Texas; rarely or sporadically eastward to southern Ontario, Missouri, Arkansas, and Louisiana. Winters in small numbers along the Atlantic and Gulf Coasts from South Carolina to southern Florida and west to southern Louisiana; and from Mexico to Central America.

STATUS: Common.

HABITAT: Occurs in almost any open habitat with scattered trees at low to moderate elevations, especially in agricultural regions. Commonly occurs near edge habitats such as shelterbelts, woodland borders, orchards, and hedgerows.

NEST: Builds nests in a variety of sites but prefers trees, when available. May nest against the trunk, in a crotch, or on a horizontal branch 8 to 40 feet above the ground in cottonwoods, oaks, sycamores, willows and other trees; if no trees are available, nests in bushes, on utility poles, or a variety of structures.

FOOD: Flycatches from a perch on poles, fence posts, or tree tops in open areas for a variety of insects; also eats millipedes, spiders, and some fruits.

REFERENCES: Beal 1912, Bent 1942, Hespenheide 1964, Johnsgard 1979, Ohlendorf 1974, Terres 1980, Terrill in Farrand 1983b.

Eastern Kingbird

Tyrannus tyrannus



L 6 3/4"

RANGE: Breeds from southwestern and north-central British Columbia, southern Mackenzie, and central Manitoba to southern Quebec and New Brunswick, south to northeastern California, northern Utah, northwestern and central New Mexico, the Gulf Coast, and Florida. Winters in South America.

STATUS: Common.

HABITAT: Frequents open areas with scattered trees or tall shrubs; forest edges or hedgerows along pastures, swamps, marshes, fields, or highways; open country around orchards; brushy streamsides; and sometimes open woodlands.

SPECIAL HABITAT REQUIREMENTS: Open habitats with perches for flycatching.

NEST: Often builds nest over water on a tree limb well away from the main trunk, or occasionally in shrubs or on an artificial structure, locating nest 10 to 20 feet, but sometimes 2 to 60 feet, above the ground. Builds nest in the crotch of a tree, on top of a dead stub, or on a fence post if no trees are available. In New England, frequently nests in the upper horizontal limbs of apple trees.

FOOD: Consumes over 200 kinds of insects and more than 40 kinds of fruits, catching most insects by hawking from a perch.

REFERENCES: Beal 1912, Bent 1942, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Terres 1980.

Gray Kingbird

Tyrannus dominicensis



RANGE: Breeds along the Atlantic and Gulf Coasts from southeastern South Carolina south to the Florida Keys, and west to southern Alabama and islands off the coast of Mississippi, south in coastal regions to South America. Winters from Hispaniola south to South America, casually in southern Florida.

STATUS: Locally common.

HABITAT: Found within the coastal zone, where it occurs in mangrove swamps, marsh edges, along roadsides, and in woodlands, groves, and yards in urban or rural areas.

SPECIAL HABITAT REQUIREMENTS: Habitats within the coastal zone.

NEST: Nests in a fork or saddle on a horizontal limb of a tree or shrub 3 to 17 feet above the ground, often hanging over water. Prefers mangroves for nesting, but also nests in oaks, acacia, sea grape, casuarina, and cabbage palm. Shows a strong attachment to the nesting site, returning yearly to the same tree or clump of trees.

FOOD: Flycatches from exposed perches for insects; also eats lizards and fruits of tropical trees.

REFERENCES: Bent 1942, Harrison 1975, Sykes in Farrand 1983b, Terres 1980.

Scissor-tailed Flycatcher

Tyrannus forficatus



L 13"

RANGE: Breeds from southeastern Colorado, southern Nebraska, and north-central Missouri south to western and southern Texas and western Louisiana; isolated breeding in northeastern Mississippi, central Tennessee, and central Iowa. Winters in southern Florida and from Mexico to Central America; casually in southern Louisiana.

STATUS: Common.

HABITAT: Occurs on plains, prairies, mesas, and flats, and around pastures, woodland clearings, ranches, and farms. Perches for long periods on tall prairie plants, limbs of dead trees, utility wires, or fences.

SPECIAL HABITAT REQUIREMENTS: Open habitats with elevated perches.

NEST: Typically nests in cottonwoods, elms, or other hardwood species, in exposed sites 6 to 30 feet above the ground. Prefers isolated trees to those growing in clumps or heavier cover; occasionally uses fence posts, telephone poles, windmill towers, or buildings for nest sites.

FOOD: Flies from a perch to catch a variety of insects, but also picks up insects from the ground. Also eats few fruits, berries, and seeds.

REFERENCES: Beal 1912, Fitch 1950, Johnsgard 1979, Oberholser 1974a.

Rose-throated Becard

Pachyramphus aglaiae



RANGE: Breeds in southeastern Arizona and in southern Texas (Cameron and Hidalgo Counties) and in Mexico and Central America. Winters in Mexico and Central America.

STATUS: Rare and local.

HABITAT: Inhabits mature groves of trees situated near flowing water, preferably stands of sycamore, cottonwood, and willow.

NEST: Builds an immense bushel-basket nest of strips of fibrous plant stems, suspending it from twigs at the end of a drooping branch 30 to 60 feet above the ground. Often places nests in sycamores but also uses cottonwoods, baldcypress, and willows. Will often build in the same site as the previous year's nest, or very close to the site.

FOOD: Perches on interior branches rather than exposed perches while feeding. Eats insects and some wild fruit.

REFERENCES: Oberholser 1974b, Phillips 1949, Phillips et al. 1964, Terres 1980, Terrill in Farrand 1983b.

Horned Lark

Eremophila alpestris



RANGE: Breeds in North America from western and northern Alaska, the Arctic Coast of northern Canada, Prince Patrick, Devon, and Baffin Islands, and northern Labrador south to Mexico, southwestern Louisiana, central Missouri, northern Alabama, and North Carolina. Winters from southern Canada south throughout the breeding range, and locally or irregularly to the Gulf Coast and southern Florida.

STATUS: Locally common.

HABITAT: Inhabits a wide variety of open habitats, from coastal dunes and alpine tundra to prairies and deserts. Prefers areas with a minimum of vegetation, such as natural or planted low-stature grasslands, cultivated and plowed fields, golf courses, airports, and other relatively barren areas. In winter, groups in small-to-enormous flocks on open, barren sites similar to its breeding habitat.

SPECIAL HABITAT REQUIREMENTS: Bare ground for nesting.

NEST: Nests in a depression on the ground, placed so that the upper edge of the nest is level with the ground surface. Often paves the nest with small pebbles along a portion of the rim. Places nest where there is little or no vegetational cover around the nest, or next to a clump of grass or a rock.

FOOD: In summer, feeds primarily on insects; in winter, it consumes seeds of grasses, weeds, and waste grains.

REFERENCES: Beal and McAtee 1912, Beason and Franks 1974, Cottam and Hanson 1938, DeGraff et al. 1980, Johnsgard 1979, Pickwell 1931, Terres 1980, Verbeek 1967.

Purple Martin

Progne subis



RANGE: Breeds from southwestern British Columbia south to Baja California; and from northeastern and east-central British Columbia and central Alberta to southern Ontario and New Brunswick south to Mexico, the Gulf Coast, and southern Florida, and west to eastern Idaho and central Utah. Local in the Rocky Mountains but avoids most other mountainous areas. Winters in South America, casually in Florida.

STATUS: Locally common; of special concern on blue list.

HABITAT: Inhabits open and cut over woodlands, open grassy river valleys, meadows around pools, shores of lakes, marsh edges, agricultural lands, saguaro deserts, parks and towns. Prefers habitats near open water. In the East, breeds almost exclusively in artificial colonial martin houses; in the West, still uses woodpecker-made cavities to a large extent.

SPECIAL HABITAT REQUIREMENTS: Large, multiroomed martin houses, tree cavities, or abandoned woodpecker holes for nesting, and open spaces for foraging.

NEST: Originally nested in cavities in large snags but is now largely dependent upon man-made martin houses. Nests colonially in houses preferably set 15 to 20 feet above the ground in open settings near suitable perches such as wires. Also uses cavities in cliffs or among loose rocks, and crevices in old buildings. In the west, still depends on old woodpecker holes for nesting; in the Arizona deserts, nests in old woodpecker holes in saguaro cacti.

FOOD: Catches flying insects on the wing for most of the diet. Also picks up a few insects and spiders from the ground.

REFERENCES: Allen and Nice 1952, Beal 1918, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Tate and Tate 1982, Terres 1980.

Tree Swallow

Tachycineta bicolor



L 5"

RANGE: Breeds from western and central Alaska and central Yukon to northern Quebec and central Labrador south along the Pacific Coast to southern California and south-central New Mexico, generally sporadic or irregular as a breeder east of the Rocky Mountain States and south of the upper Mississippi and Ohio Valleys, or along the Atlantic Coast south of Massachusetts. Winters from southern California, southwestern Arizona, Texas, the Gulf Coast, and the Atlantic Coast from New York south to Central America.

STATUS: Common.

HABITAT: Prefers open woodlands near ponds, small lakes, or marshes. Occurs around farmlands, river bottomlands, beaver ponds, wooded swamps, and marshes where dead standing trees are in or near water.

SPECIAL HABITAT REQUIREMENTS: Cavities for nesting; suitable cavity trees must have a minimum dbh of 10 inches, and open feeding areas such as meadows, marshes, or open water.

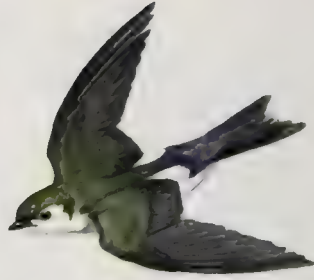
NEST: Prefers to nest in natural cavities and abandoned woodpecker holes, but if nesting holes are scarce, will accept nest boxes placed in open fields or use crevices in buildings. Uses cavities in the trunk or limb of live or dead trees, especially if the cavity is 3 to 15 feet above water. Usually nests singly but is loosely colonial if there are abundant suitable cavities and a good food supply.

FOOD: Feeds mostly on flying insects over open areas. In early spring and in cold weather when insects are scarce, subsists on wild berries and seeds, especially bayberries.

REFERENCES: Beal 1918, Chapman 1955, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Scott et al. 1977, Terres 1980, Thomas et al. 1979.

Violet-green Swallow

Tachycineta thalassina



L 4¾"

RANGE: Breeds from central Alaska, central Yukon, and extreme southwestern Mackenzie south to Mexico, and east to southwestern Saskatchewan, western South Dakota, and western Nebraska. Winters from central coastal and southern California south to Central America.

STATUS: Common.

HABITAT: Inhabits coniferous, deciduous, and mixed forests, preferring open or broken woods, or the edges of dense woodlands. Occurs around towns, in woodland clearings, especially near lakes and streams, and if snags are present, in canyons, and in mountains from the foothills to near timberline.

SPECIAL HABITAT REQUIREMENTS: Cavities or crevices for nesting and open terrain or forest openings for feeding.

NEST: Builds nests in old woodpecker holes, natural tree cavities, crevices in rocky cliffs, nesting boxes, niches of old buildings, and when cavities are scarce, in old nests of cliff swallows and burrows of bank swallows. In Colorado, prefers cavities in ponderosa pine but also nests in aspen and other trees.

FOOD: Consumes only insects, which catches and eats while on the wing.

REFERENCES: Bailey and Niedrach 1965, Beal 1918, Bent 1942, Combellack 1954, Johnsgard 1979, Scott et al. 1977, Terres 1980.

Northern Rough-winged Swallow

Stelgidopteryx serripennis



L 4¾"

RANGE: Breeds from southeastern Alaska, central British Columbia, and southern Alberta to southwestern Quebec and central Maine south to Central America and south-central and southwestern Florida. Winters from southern Texas, southern Louisiana, and southern Florida south to Mexico and Central America.

STATUS: Fairly common.

HABITAT: Inhabits open country, including open woodlands, wherever a suitable nest site near water can be found. In the East, frequents rocky gorges, shale banks, stony road cuts, railroad embankments, river valleys, and stream banks. In the Midwest and West, often found around gravel pits, stream banks, and other exposed banks of sand, dirt, or gravel.

SPECIAL HABITAT REQUIREMENTS: Suitable nest sites preferably near, but up to 1/2 mile from water.

NEST: Excavates nests in banks of clay, sand, or gravel or uses abandoned bank swallow or kingfisher burrows and sometimes natural rock crevices, drainpipes, culverts, cracks in bridges, and crevices in buildings. May nest singly, in scattered groups, or in small colonies; tends to be more colonial in the western part of its range.

FOOD: Feeds on the wing, catching primarily flies and other flying insects.

REFERENCES: Beal 1918, DeGraff et al. 1980, Johnsgard 1979, Lunk 1962.

Bank Swallow

Riparia riparia



L 4¾"

RANGE: Breeds from western and central Alaska and central Yukon to central Quebec and southern Labrador, south to southern California, western Nevada, southern New Mexico, southern Texas, northern Alabama, eastern Virginia, and casually, northwestern North Carolina and south-central South Carolina. Winters in South America.

STATUS: Locally common; population is declining over parts of its range.

HABITAT: Prefers grasslands and cultivated fields but uses a variety of open habitats, usually near water and suitable nest sites. Nests in riverbanks, borrow pits, gravel pits, road cuts, sand banks and other exposed banks of sand, gravel or clay.

SPECIAL HABITAT REQUIREMENTS: Vertical banks of sand, gravel, or clay in an open habitat, preferably near lakes, ponds, or marshes.

NEST: Excavates a burrow near the top of a vertical bank (or repairs an existing burrow) ranging from 9 inches to 6 feet, but generally about 2 feet, in length. Forms dense colonies, with up to several hundred nests in a bank.

FOOD: Catches primarily flies while flying over water or grasslands, especially pastures.

REFERENCES: Allen 1933, Beal 1918, Beyer 1938, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Peterson 1955, Tate and Tate 1982.

Cliff Swallow

Hirundo pyrrhonota



L 5"

RANGE: Breeds from western and central Alaska and central Yukon to northern Ontario, southern Quebec and New Brunswick south to Mexico, southwestern Louisiana, northern portion of the Gulf States and southern North Carolina; also in the Lake Okeechobee region of southern Florida. Winters in South America.

STATUS: Common in the West, locally fairly common in the East; overall populations are stable or increasing, except in some northeastern States where it is of special concern on the blue list for declining species.

HABITAT: Originally restricted to the vicinity of cliffs and banks; now occurs over open country around farmlands, towns, bridges, dams, freeway overpasses, and other areas near mud supplies and potential nest sites.

SPECIAL HABITAT REQUIREMENTS: A vertical substrate with an overhang for nest attachment, a supply of mud suitable for nest construction, fresh water with a smooth surface for drinking, and an open foraging area near the nest site.

NEST: Originally nested on bluffs, cliffs, deep gorges in mountains, and sometimes on the side of large pine trees and in caves; has adapted to building its gourdlike mud nests under the eaves of, or in, buildings, under bridges, in culverts, on the face of dams, and under freeway overpasses. Forms colonies of up to several hundred nests in favorable locations.

FOOD: Consumes insects caught while flying high, often above 100 feet, as nearly 100 percent of the diet.

REFERENCES: Beal 1918, Bent 1942, DeGraff et al. 1980, Emlen 1954, Forbush and May 1955, Johnsgard 1979, Mayhew 1958, Samuel 1971, Tate and Tate 1982.

Cave Swallow

Hirundo fulva



L 4¾"

RANGE: Breeds from Carlsbad Caverns in southeastern New Mexico and from western and south-central Texas south through Mexico. Winter range is unknown.

STATUS: Locally fairly common; range is expanding as it adapts to human-altered environment.

HABITAT: Originally restricted to open country in the vicinity of limestone caves and sinkholes; has adapted its nesting habits to artificial structures. Now also nests around culverts and bridges in the northern part of its range where water and mud are available.

SPECIAL HABITAT REQUIREMENTS: Extensive roughened or pitted surfaces for nesting in caves, water for drinking, and mud suitable for nest construction.

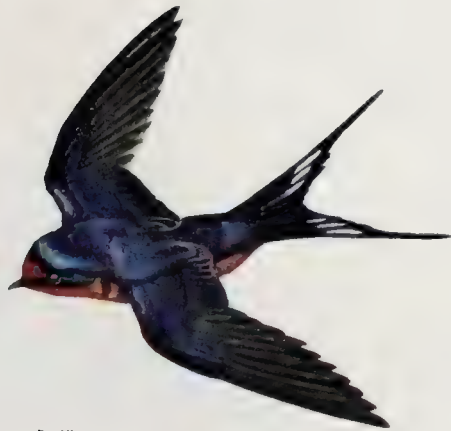
NEST: Forms colonies and in caves, tends to build its mud nests in isolated crevices and pockets, or under overhanging ledges. Also nests in sinkholes, in highway culverts, and under bridges. May reuse nest year after year and will sometimes share the same nest site with barn swallows.

FOOD: Needs a source of water, such as a seep, spring, open water tank, or pond for drinking. (The diet of this swallow in the United States is currently unknown.)

REFERENCES: Martin 1974, 1981, Selander and Baker 1957, Wauer and Davis 1972.

Barn Swallow

Hirundo rustica



L 6"

RANGE: Breeds from south-coastal and southeastern Alaska and southern Yukon across to central Manitoba, northern Ontario, and southern Quebec south to Mexico, the Gulf Coast, north-central Florida, and southern North Carolina. Winters in Central and South America, casually north to the southwestern United States and southern Florida.

STATUS: Common.

HABITAT: Occurs virtually throughout the whole United States wherever suitable nest sites are found, but favors farmlands, open forests, rural, and suburban areas.

SPECIAL HABITAT REQUIREMENTS: Overhead protection, especially buildings, for nesting.

NEST: Originally nested on cliffs and in caves and rock crevices in mountains, along rocky coasts, and on high shores of lakes and rivers. Still uses such sites in the north and on the Pacific Coast, but in other areas nests on horizontal beams or ledges inside barns or other buildings, or under bridges, culverts, or wharves. Usually nests colonially.

FOOD: Prefers to feed over water or fields, catching flying insects (especially flies) on the wing.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Samuel 1971.

Gray Jay

Perisoreus canadensis



RANGE: Breeds from western and central Alaska, northern Mackenzie, and southwestern Keewatin across to northern Quebec and northern Labrador, south to northern California, central Idaho, east-central Arizona, Black Hills of South Dakota, central Saskatchewan, northern Minnesota, southern Ontario, and northern New England. Winters generally throughout the breeding range.

STATUS: Locally common.

HABITAT: Inhabits northern coniferous forests, especially dense spruce and pine. Occasionally occurs in mixed forests and deciduous woodlands near coniferous forests.

SPECIAL HABITAT REQUIREMENTS: Conifer forests.

NEST: Builds nest in late winter while there is still deep snow in the woods, typically in a crotch or on a horizontal branch near the trunk of a conifer, often less than 10 feet but up to 30 feet above the ground. Usually hides well.

FOOD: Regularly catches food, producing a special saliva that helps bind the food together, so it can be firmly held in conifer foliage. Is omnivorous and typically eats insects, conifer seeds, berries, young birds, small mammals, lichens, fungi, and carrion. Commonly steals food from campers.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Goodwin 1976, Johnsgard 1979, Ouellet 1970, Rutter 1969.

Steller's Jay

Cyanocitta stelleri



L 11"

RANGE: Resident from south-coastal and southeastern Alaska to southwestern Alberta south to southern California, Arizona, central New Mexico, Central America, and western Texas, and east to western Montana and western Nebraska.

STATUS: Common.

HABITAT: Generally inhabits coniferous forests throughout its range, but occasionally occurs in mixed and deciduous woodlands, and ventures into orchards and gardens. Is especially frequent in the ponderosa pine zone but limited numbers occur in the pinyon-juniper and spruce-fir zones. Favors edges of forest openings over extensive, unbroken woodlands.

SPECIAL HABITAT REQUIREMENTS: Predominately coniferous woodlands.

NEST: Usually builds nest on a horizontal branch of a conifer from 8 to 40 feet, but up to 100 feet, above the ground. Occasionally locates nest in a shrub or tree cavity.

FOOD: Usually forages on the ground and in trees for seeds, nuts, acorns, fruits, insects, spiders, and bird eggs and nestlings.

REFERENCES: Gibson in Farrand 1983b, Goodwin 1976, Johnsgard 1979, Wilmore 1977.

Blue Jay

Cyanocitta cristata



L 10"

RANGE: Resident from extreme east-central British Columbia and central and southeastern Alberta to southern Quebec and Newfoundland south to central and southeastern Texas, the Gulf Coast, and southern Florida, and west to eastern Montana and east-central New Mexico. Northern populations are partly migratory to the southern parts of the breeding range.

STATUS: Common.

HABITAT: Inhabits deciduous and mixed woodlands, especially preferring those with oak, beech, and hickory, but also occurs in coniferous forests, preferably where pines predominate. Also frequents wooded islands, farms, gardens, parks, cities — almost anywhere trees are found in grassland areas.

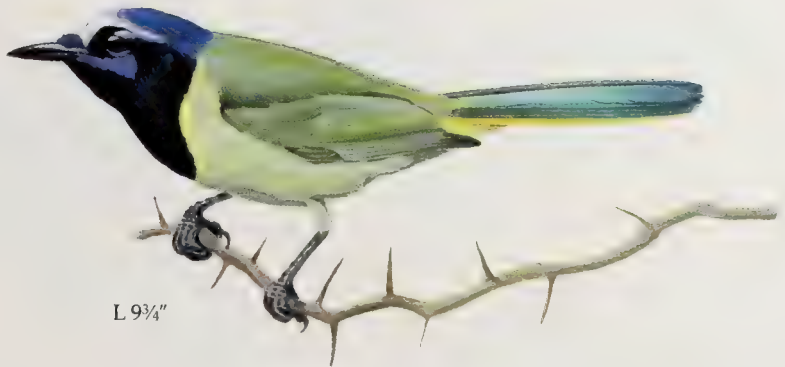
NEST: Hides nest well in the fork, crotch, or outer branches of trees, occasionally in shrubs, typically from 10 to 25 feet, but ranging from 5 to 50 feet, above the ground. Prefers conifer thickets in mixed woodlands for nesting.

FOOD: Forages from the tree tops to the ground for its food, which consists of 76 percent vegetable and 24 percent animal matter. Feeds omnivorously, primarily on mast but also takes a variety of other foods. Also eats grains, weed seeds, wild fruits, insects, a few mice, young birds and eggs, fish, salamanders, and crustaceans. Is easily drawn to bird feeders.

REFERENCES: Beal 1904, DeGraff et al. 1980, Goodwin 1976, Johnsgard 1979, Wilmore 1977.

Green Jay

Cyanocorax yncas



RANGE: Resident in southern Texas; also from Mexico to South America.

STATUS: Fairly common.

HABITAT: Found in dense thickets and woodlands along the lower Rio Grande, in mesquite woodlands, and thickets of mesquite, retama, and hackberry. In winter, wanders in small flocks in more open country, frequenting woods of huisache, ebony blackbean, and anacua.

NEST: The nest is built in a fork or outer branches of small trees or bushes from 5 to 15 feet above the ground, in dense woods or thickets along streams.

FOOD: Feeds omnivorously, including insects, spiders, seeds, acorns, palmetto fruit, and eggs and young of birds in the diet.

REFERENCES: Cottam and Knappen 1939, Oberholser 1974b, Terres 1980, Wilmore 1977.

Scrub Jay

Aphelocoma coerulescens



L 10"

RANGE: Resident from southwestern Washington to southern Wyoming and Colorado south to Baja California, western and west-central Texas, and Mexico; also on Santa Cruz in the Channel Islands in California, and in central Florida.

STATUS: Locally common; population is declining in Florida because of clearing and development of orange groves.

HABITAT: Inhabits a variety of brushy areas from dense chaparral, open woodlands and residential areas in the Pacific States to pinyon-juniper, scrub oak, and less frequently mixed oak and ponderosa pine in the interior West, and humid scrub-oak communities in Florida. Prefers borders of brushy ravines and wooded creek bottoms. In Florida, usually found near small openings or at the edge of the scrub rather than in dense, unbroken scrub.

SPECIAL HABITAT REQUIREMENTS: Scrub habitats.

NEST: Builds nest in pinyons, oaks, tall shrubs, or vine tangles, generally less than 10 feet, but up to 30 feet, above the ground. Usually nests singly, but in Florida may nest in scattered colonies with up to 6 nests in small tracts of scrub.

FOOD: Consumes many kinds of insects and other invertebrates. Also eats acorns, seeds of palmetto, grains, fruits, mice, eggs and nestlings of birds, small reptiles, and frogs.

REFERENCES: Goodwin 1976, Harrison 1975, Johnsgard 1979, Tate and Tate 1982, Terres 1980, Terrill in Farrand 1983b, Wilmore 1977.

Gray-breasted Jay

Aphelocoma ultramarina
(formerly Mexican Jay)



L 10¾"

RANGE: Resident from central Arizona, southwestern New Mexico, and western Texas south to Mexico.

STATUS: Common.

HABITAT: Inhabits canyons and hillsides of oak and pine-oak woodlands, adjacent riparian forests, and occasionally ventures into adjacent pure pine woodlands or more open scrub, from 2,000 to 9,000 feet in elevation.

SPECIAL HABITAT REQUIREMENTS: Live oaks within its home range.

NEST: Builds nest in a fork, crotch, or on a horizontal branch of oaks or pines, typically 10 to 25 feet, but ranging from 6 to 54 feet above the ground. May nest singly or in loose colonies, and participates in communal nest building.

FOOD: Usually forages on the ground and in trees for acorns, insects, lizards, eggs and young birds, fruits, and seeds.

REFERENCES: Goodwin 1976, Gross 1949, Terres 1980, Wilmore 1977.

Pinyon Jay

Gymnorhinus cyanocephalus



L 9"

RANGE: Breeds from central Oregon to western South Dakota, south to Baja California, northwestern and east-central Arizona, central New Mexico, and western Oklahoma. Winters throughout the breeding range and irregularly from southern Washington to northwestern Montana south to Mexico and central Texas.

STATUS: Common.

HABITAT: Typically inhabits pinyon-juniper woodlands of the foothills and lower mountain ranges in the West, but also occurs in open ponderosa pine forests where the soil is dry and trees are small and scattered. Locally nomadic outside the nesting season in response to fluctuating food supplies; during years of a poor seed crop, may move in flocks hundreds of miles to find food.

SPECIAL HABITAT REQUIREMENTS: Open woodlands for nesting and an adequate supply of seeds, especially pinyon nuts.

NEST: Usually nests in scattered colonies of up to 100 birds, usually with just one nest per tree. Builds nest away from the center of a tree on a low, southerly facing horizontal limb, and generally 6 to 20 feet, but up to 85 feet, above the ground. Pinyons, junipers, ponderosa pines, and scrub oaks are common nest trees.

FOOD: Forages in trees and on the ground, principally for seeds, especially pinyon nuts, but also seeds of ponderosa pines and other conifers, and caches them for use during the next breeding season. It also eats fruits, berries, insects, and eggs and nestlings of small birds.

REFERENCES: Balda and Bateman 1972, Goodwin 1976, Johnsgard 1979, Terres 1980, Wilmore 1977.

Clark's Nutcracker

Nucifraga columbiana



L 11"

RANGE: Resident from central British Columbia and southwestern Alberta to western and southeastern Wyoming, south through the mountains of Washington, Oregon, California, and Nevada to Baja California, and in the Rockies to east-central Arizona and southern New Mexico. Occasionally wanders during nonbreeding season to lower mountains and lowlands beyond breeding range.

STATUS: Common.

HABITAT: Prefers high-altitude rocky sites with open or broken coniferous forest and clearings, but occurs in the mountains from 3,000 to 13,000 feet. Inhabits a variety of coniferous forest types including ponderosa pine, pinyon-juniper, and spruce-fir.

SPECIAL HABITAT REQUIREMENTS: Seeds of pines for food.

NEST: Nests mostly between 6,000 and 8,000 feet in elevation in a wind-sheltered site. Builds nest in a conifer, well out on a branch or in a bushy top from 7 to 150 feet above the ground.

FOOD: Forages on the ground and in trees, primarily on the seeds of conifers and on insects. Also eats seeds of lupine, oats, grains, berries, small mammals, eggs and nestlings of birds, and carrion.

REFERENCES: Bevier in Farrand 1983b, Cottam 1945, Goodwin 1976, Mewaldt 1956, Terres 1980, Verner and Boss 1980, Wilmoer 1977.

Black-billed Magpie

Pica pica

RANGE: Resident from south-coastal and southern Alaska to northern Alberta, central Manitoba, and western Ontario south to northeastern and east-central California and south-central Nevada, across to western and northeastern Oklahoma. Casual north and east of range in fall and winter.

STATUS: Common.

HABITAT: Typically inhabits open country with short, scattered, clumped or grazed vegetation, or exposed ground, and with patches of scrub, large bushes, or trees. Avoids dense forests and strictly desert regions. Found nearly up to timberline in the mountains; frequents a variety of open habitats including sagebrush, agricultural lands, pastures, grasslands, forest edges, streamsides with tall thickets and scattered trees, open woodlands, and urban areas.

SPECIAL HABITAT REQUIREMENTS: Open country for foraging, trees or large bushes for nesting and cover.

NEST: Builds a bulky stick nest from a few feet to 25 feet above the ground in a variety of trees or tall bushes, especially thorny ones. Nests in small, scattered colonies along streams, in woods, or in thickets, less often on buildings, cliff ledges, high banks, or on the ground among bushy cover. Sometimes reuses the old nest but usually builds a new nest each year.

FOOD: Forages mainly on the ground, sometimes in trees or shrubs, for insects, especially grasshoppers. Also eats snails, slugs, millipedes, spiders, fishes, reptiles, amphibians, young birds and eggs, small mammals, carrion, and wild and cultivated fruits.

REFERENCES: Ballard in Farrand 1983b, Goodwin 1976, Johnsgard 1979, Kalmbach 1927, Linsdale 1937, Terres 1980, Wilmore 1977.

Yellow-billed Magpie

Pica nuttalli



Yellow-billed

L 16"

Black-billed

L 18"

RANGE: Resident in California in the Sacramento and San Joaquin Valleys, and in valleys of the coast ranges from San Francisco Bay south to Santa Barbara County.

STATUS: Common.

HABITAT: In farming country, foothills, and valleys, inhabits broken oak woodland interspersed with grasslands or cultivated lands, open riparian woodland, oak savannah, and vacant city lots. Avoids areas with high strong winds, cold snowy winters, and very dry hot summers. Prefers tall trees in a linear arrangement, such as trees bordering streams, parklike groves, or orchards.

SPECIAL HABITAT REQUIREMENTS: Tall trees near open water for nesting.

NEST: Believed to mate for life; breeds in small loose colonies, with each pair in a different tree. Prefers tall trees usually about 50 feet. Builds nest near the tree top on a small limb far out from the trunk, sometimes in a mistletoe clump. Occasionally reuses nest, but usually builds a new one each year. Locates nest in sycamore, oak, cottonwood, and digger pine.

FOOD: Consumes a diet of about half insects, especially grasshoppers, but also eats grains, acorns, cultivated and wild fruits, and carrion.

REFERENCES: Goodwin 1976, Kalmbach 1927, Linsdale 1937, Terres 1980, Verbeek 1973, Wilmore 1977.

American Crow

Corvus brachyrhynchos



L 17"

RANGE: Breeds from north-central British Columbia and southwestern Mackenzie to central Quebec and southern Newfoundland south to Baja California, central Arizona, southern New Mexico, central and southeastern Texas, the Gulf Coast, and southern Florida. Winters from southern Canada south throughout the breeding range.

STATUS: Common.

HABITAT: Most often inhabits open and semiopen habitats, favoring open deciduous, coniferous, and mixed forests, wooded river bottoms, groves, orchards, woodlands adjacent to agricultural land, suburban areas, parks, and woodlots.

NEST: Builds a nest, a large platform of sticks, usually on a horizontal branch or in a crotch of a tree near the trunk, 10 to 75 feet above the ground. Prefers conifers and oaks as nest trees, but where trees are lacking, will build nests on the ground, on shrubs, or on telephone pole crossbars.

FOOD: Prefers to forage in cultivated fields. Has an omnivorous diet that is three-fourths vegetable foods, including cultivated grains, seeds, wild and cultivated fruits, and nuts. Also eats insects, millipedes, spiders, small crustaceans, small reptiles, frogs, small mammals, eggs and young of birds, and carrion.

REFERENCES: DeGraff et al. 1980, Goodwin 1976, Johnsgard 1979, Lehman in Farrand 1983b, Wilmore 1977.

Northwestern Crow

Corvus caurinus



L 14½"

RANGE: Resident along the Pacific Coast from south-coastal and southeastern Alaska south to the Puget Sound area in northwestern Washington.

STATUS: Common.

HABITAT: Occurs along the coast, rarely straying farther than a mile from tidal waters, where it inhabits saltwater beaches, towns, and the wooded shores of bays, especially where there are small coniferous trees.

NEST: Nests in scattered pairs or in loose colonies, usually in a crotch of a low tree or bush 10 to 20 feet, but up to 70 feet, above the ground. Occasionally builds nest on the ground under overhanging boulders, under bushes or windfalls, on the side of a sandy bank, or in a hole in a cliff. Will locate nest in apple, hemlock, Douglas-fir, and spruce trees.

FOOD: Scavenges refuse from beaches, along with mollusks and other shellfishes. Forages for insects, especially grasshoppers, in nearby cultivated fields. Also eats crabs, mussels, dead fish and other carrion, eggs of other birds, and wild and cultivated fruits.

REFERENCES: Bent 1946, Goodwin 1976, Terres 1980, Wilmore 1977.

Fish Crow

Corvus ossifragus



L 15"

RANGE: Resident from New York and Massachusetts south along the Atlantic Coast to southern Florida and west to southern Texas; inland along major river systems to southern Illinois and east-central Oklahoma.

STATUS: Locally common; range is extending northward and into drier regions.

HABITAT: Inhabits low coastal areas, especially wooded marine shorelines, coastal marshes and beaches, brackish bays, fertile farmlands up to 100 miles from the coast, inland wetlands, and forests near rivers and lakes. Occasionally occurs in pine forests, orchards, old dry fields, and abandoned farmlands overgrown with natural grasses and pines.

NEST: Nests singly or in loose colonies of 2 to 4 pairs, each nesting in a separate tree. Builds nest near the tops of trees, especially pines, usually 10 to 90 feet, but up to 150 feet, above the ground; rarely in tall shrubs. Usually locates nest near water in a large fork or on a horizontal limb close to the trunk.

FOOD: Gathers food from the ground or trees, most commonly from tidal flats, beaches, rookeries, and riverbanks. Eats a diet that includes crabs, shrimps, and other crustaceans; stranded and dead fish; insects; eggs and young of birds; small reptiles; wild fruits; cultivated grains; seeds; and carrion.

REFERENCES: DeGraff et al. 1980, Goodwin 1976, Johnsgard 1979, Wilmore 1977.

Chihuahuan Raven

Corvus cryptoleucus
(formerly White-necked Raven)



L 17½"

RANGE: Resident from south-central and southeastern Arizona, central and northeastern New Mexico, northeastern Colorado, and south-central Nebraska south to Mexico, and east to western Kansas and central Texas. (Northeastern populations, especially those in Nebraska and Kansas, migrate southward in winter.)

STATUS: Locally common.

HABITAT: Favors open, arid grasslands interspersed with yucca, mesquite, and cactus. Also occurs in deserts, on the open plains, and in arid farmlands, extending into the foothills. Outside the breeding season, often forms large flocks and roosts communally in canyons and gulches.

NEST: Usually builds nest in isolated trees or bushes, 4 to 40 feet above the ground; often uses same nest year after year. Uses sycamore, mesquite, willow, oak, yucca, cottonwood and other species for nest sites, but also nests on utility poles and windmill towers.

FOOD: Typically eats insects, especially grasshoppers and beetles, cultivated grains, small reptiles, fruits of cacti, carrion, eggs and young of birds, and scraps of human food.

REFERENCES: Bent 1946, Goodwin 1976, Johnsgard 1979, Terrill in Farrand 1983b, Wilmore 1977.

Common Raven

Corvus corax



L 21"

RANGE: Resident from Alaska and northern Canada south through the western United States to Baja California and Mexico, and east to the eastern edge of the Rockies, western Oklahoma, and central Texas; east of the Rockies, south to central Saskatchewan, northern Wisconsin, southern Ontario, Vermont, and southeastern Maine; also locally in the Appalachians to northwestern Georgia.

STATUS: Common to locally common; reinvading its historic range and colonizing new areas.

HABITAT: Occurs in a wide variety of habitats but is most often found in open woodlands and mountainous and coastal regions. Inhabits rocky seacoasts, steep canyons, boreal forests, deserts, foothills, mountains, arctic tundra, and wooded marine islands. Tends to avoid extensive, dense forests.

SPECIAL HABITAT REQUIREMENTS: Cliff ledges or tall trees for nesting.

NEST: Usually builds nest high up in a tall coniferous tree or on a cliff ledge that is sheltered overhead and undercut or nearly vertical below. Generally selects locations inaccessible to humans and will sometimes use the same site in successive years.

FOOD: Scavenge for road kills along highways, and eats small mammals, reptiles, frogs, eggs, young and wounded birds, insects, mollusks, cultivated grains, mast, fruits, and other plant material. Eats all types of carrion, from small to large mammals to fishes.

REFERENCES: DeGraff et al. 1980, Goodwin 1976, Harlow et al. 1975, Hooper 1977, Johnsgard 1979, Knight and Call 1980, Terrill in Farrand 1983b, White and Cade 1971, Wilmore 1977.

Black-capped Chickadee

Parus atricapillus



L 4½"

RANGE: Resident from western and central Alaska, Saskatchewan, southern Quebec, and Newfoundland south to northwestern California, northeastern Nevada, central New Mexico, northeastern Oklahoma, central Indiana, and northern New Jersey, and in the Appalachians at higher elevations. Wanders irregularly south in winter.

STATUS: Common.

HABITAT: Prefers mixed woodlands but also inhabits deciduous and coniferous forests. Will inhabit dense woodlands to thickets, orchards, and urban areas, wherever suitable nesting cavities exist or can be excavated.

SPECIAL HABITAT REQUIREMENTS: Comparatively open sites near deep woods, and dead standing trees larger than 4 inches dbh for nesting and feeding.

NEST: Usually excavates own nest holes in soft decayed wood of a dead tree or branch stub; will use existing cavities of other birds or bird houses. Prefers to nest in tree species that occur in early seral stages such as aspen, paper birch, yellow birch, willow, basswood, maple, and white ash. Favors trees adjacent to open areas in forest or edge situations for nest sites. Generally roosts in dense foliage rather than cavities.

FOOD: Forages from the ground to the tree tops for a variety of insects, conifer seeds, and fruits.

REFERENCES: Bailey and Niedrach 1965, Bent 1946, Brewer 1961, Forbush and May 1955, Johnsgard 1979, Martin et al. 1951, Odum 1941a, 1941b, 1942, Thomas et al. 1979.

Carolina Chickadee

Parus carolinensis



RANGE: Resident from southern Kansas, central Illinois, central Ohio, and central New Jersey south to central and southeastern Texas, the Gulf Coast and northern peninsular Florida. Wanders casually to the north and southward.

STATUS: Common.

HABITAT: Inhabits coniferous and deciduous woodlands; prefers forest and forest edge habitats similar to, but more moist and warm than, those preferred by the black-capped chickadee. Also frequents swamps, thickets, second-growth woodlands, parks, and brushy areas.

SPECIAL HABITAT REQUIREMENTS: Standing dead trees for excavating cavities.

NEST: Usually excavates nest holes in dead, decayed tree trunks or in dead limbs of living trees. Occasionally nests in old woodpecker holes or natural cavities. (The nest and eggs of this species cannot be distinguished from those of the black-capped chickadee.) Chooses willow, pine, cottonwood, poplar, pear, and cherry for nest trees.

FOOD: Has very similar food habits to those of the black-capped chickadee.

REFERENCES: Bent 1946, Brewer 1961, 1963, Johnsgard 1979, Pitts 1976.

Mexican Chickadee

Parus sclateri



L 4 1/4"

RANGE: Resident in Mexico, the Chiricahua Mountains of southeastern Arizona, and the Animas Mountains of southwestern New Mexico.

STATUS: Locally common.

HABITAT: Occurs in almost any habitat with conifers up to 7,000 to 8,000 feet in elevation, even where trees are sparse, but prefers pine-oak woodlands and montane pine and spruce-fir forests, primarily in mesic habitats. Outside the breeding season, may also be found in groves of Arizona cypress at lower elevations.

SPECIAL HABITAT REQUIREMENTS: Dead trees for cavity nest.

NEST: Excavates its own cavity in a dead stub, tree trunk, or branch.

FOOD: Probably eats insects and seeds similar to other chickadees. (No specific information is available on food habits).

REFERENCES: Bent 1946, Harrison 1979, Phillips et al. 1964, Terres 1980.

Mountain Chickadee

Parus gambeli



L 4¼"

RANGE: Resident from northwestern and central British Columbia, southwestern Alberta, western and south-central Montana, and Colorado south to Baja California, southern Nevada, central and southeastern Arizona, southern New Mexico, and extreme western Texas.

STATUS: Common.

HABITAT: Inhabits open coniferous forests from 6,000 to 11,000 feet in elevation. In winter, often ranges downslope to the foothills, frequenting oaks, and cottonwoods and willows along streams.

SPECIAL HABITAT REQUIREMENTS: Decayed trees or stubs for excavating nests, or old cavity nests.

NEST: Usually nests in natural cavities or abandoned woodpecker holes, but will excavate its own holes in rotted wood. Many nest in aspen trees associated with a conifer forest.

FOOD: Gleans much of its food from foliage, especially large volumes of adult and larval insects. When densities of lodgepole needle miners are high, consumes these insects for much of its diet. Also eats seeds, spruce buds, and fruits.

REFERENCES: Bent 1946, DeWeese et al. 1979, Phillips et al. 1964, Scott et al. 1977, Telford and Herman 1963, Winternitz 1973.

Siberian Tit

Parus cinctus
(formerly Gray-headed Chickadee)



L 4¾"

RANGE: Resident from northern Alaska east across northern Yukon to northwestern Mackenzie, and south locally to western and central Alaska.

STATUS: Uncommon.

HABITAT: Inhabits spruce, willow, aspen, and birch stands along rivers at the northern limit of the boreal forest. During winter, wanders widely through river valleys.

SPECIAL HABITAT REQUIREMENTS: Natural cavities, abandoned woodpecker holes, or trees with soft, dead wood for nesting.

NEST: Builds nest inside an abandoned woodpecker hole or a natural cavity in a tree or stump; may excavate a cavity in trees with soft, dead wood.

FOOD: Eats adult, larvae, and eggs of insects in summer, and seeds of conifers and berries in winter.

REFERENCES: Bent 1946, Gibson in Farrand 1983b, Terres 1980.

Boreal Chickadee

Parus hudsonicus



L 4¼"

RANGE: Resident from western and central Alaska and central Yukon to northern Ontario and Labrador, south to extreme north-central Washington, northwestern Montana, northern Minnesota, northern Michigan, northern New York, Maine, and Nova Scotia. After the breeding season, wanders irregularly to the south.

STATUS: Fairly common.

HABITAT: Associated with northern coniferous forests, where it inhabits spruce, balsam, and dense pine woodlands, white cedar and hemlock swamps, bogs, and occasionally birch and streamside willows.

SPECIAL HABITAT REQUIREMENTS: Available cavities, or decaying trees with soft heartwood and hard exterior layers and bark for excavating nest cavities.

NEST: Excavates nest cavity in trees or stubs, preferably with soft and decayed heartwood but hard outer layers; it may use natural cavities or old woodpecker holes. Uses cavity opening from 1 to 10 feet above the ground, facing upward rather than laterally like the nests of other chickadees. Selects nest sites more for the softness of the heartwood than for the species of tree.

FOOD: Consumes adults, larvae, pupae, and eggs of insects found by gleaning and probing tree trunks, bark crevices, and foliage. Also extracts seeds from cones, and eats fruits.

REFERENCES: Bent 1946, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, McLaren 1975, Terres 1980.

Chestnut-backed Chickadee

Parus rufescens



L 4¼"

RANGE: Resident from south-central and southeastern Alaska, western British Columbia, northern Idaho, western Alberta, and northwestern Montana south through the coast ranges to southern California and through the Cascades and Sierra Nevadas to central California.

STATUS: Common; has extended its range in California in the past 20 years.

HABITAT: Prefers low-elevation, coastal, mesic coniferous forests of pines, cedar, tamarack, and hemlock. Also inhabits along streams and in adjacent deciduous woodlands.

SPECIAL HABITAT REQUIREMENTS: Available tree cavities or rotted snags suitable for nest excavation.

NEST: Builds nest in natural cavities, or abandoned woodpecker holes, or excavates cavities in soft, rotted tree stubs. Prefers pine, oak, and Douglas-fir snags.

FOOD: Gleans much of its food from tree trunks, but also from rotting logs on the ground. Primarily eats insects but also takes spiders, some fruit pulp, and conifer seeds.

REFERENCES: Beal 1907, Bent 1946, Grinnell and Miller 1944, Root 1964, Terres 1980.

Bridled Titmouse

Parus wollweberi



L 4½"

RANGE: Resident from central and southeastern Arizona and southwestern New Mexico, south locally to Mexico.

STATUS: Common.

HABITAT: Generally found in oak woodlands and pine-oak associations from 5,000 to 7,000 feet in elevation. In winter, may move down slope along streams where cottonwoods are present.

SPECIAL HABITAT REQUIREMENTS: Natural cavities in living or dead oaks.

NEST: Usually builds nest in natural cavities of dead and living oak, but will also use cavities in cottonwood, willow, and mesquite.

FOOD: Spends much of its time foraging in crevices in bark, on tree trunks, and on branches, presumably for adults, larvae, and eggs of insects.

REFERENCES: Bent 1946, Phillips et al. 1964, Terres 1980.

Plain Titmouse

Parus inornatus



L 5"

RANGE: Resident from southern Oregon, northeastern Nevada, southern Wyoming, and western Oklahoma, south to Baja California, central and southeastern Arizona, southern New Mexico, and extreme western Texas.

STATUS: Common.

HABITAT: In California, prefers oak woodlands; in the Great Basin and desert mountain ranges, occurs in pinyon-juniper woodlands. Greatest numbers inhabit evergreen trees in dry woodlands of the Southwest.

SPECIAL HABITAT REQUIREMENTS: Nest and roost cavities.

NEST: Usually builds nest in natural cavities or old woodpecker holes, primarily in oak trees; will also use nest boxes if available. Is capable of excavating its own cavity in rotted wood.

FOOD: Gleans much of its food, which is predominantly insects, from limbs, twigs, and from the ground. Also eats leaf galls, weed seeds, pinyon nuts, acorns, oats, and cherries.

REFERENCES: Bent 1946, Dixon 1949, Johnsgard 1979, Root 1964, Terres 1980, Wetmore 1964.

Tufted Titmouse

Parus bicolor



RANGE: Resident from northeastern Nebraska, central and eastern Iowa, southern Wisconsin, northern Ohio, southern Ontario, central New York, western Massachusetts, and southwestern Connecticut south to western Texas, the Gulf Coast, and southern Florida, and west to central Kansas, eastern Oklahoma and eastern Mexico.

STATUS: Common.

HABITAT: Associated with eastern coniferous and deciduous forests, where it prefers woodland swamps and river bottoms. Also occurs in orchards, low, rich woodlands, woodlots, city parks, and suburban areas.

SPECIAL HABITAT REQUIREMENTS: Natural cavities or woodpecker holes for nesting.

NEST: Usually nests in natural tree cavities or old woodpecker holes, generally 10 to 20 feet, but ranging from 3 to 90 feet, above the ground. Occasionally nests in bird boxes.

FOOD: Gleans food from branch and leaf surfaces during spring and summer and from branch surfaces and the ground in winter. Feeds primarily on insects, especially caterpillars; also eats snails; spiders; berries; seeds of sumac, yellow-poplar, alder, poison ivy, and bayberry; and some mast.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Gillespie 1930, Johnsgard 1979, Laskey 1957, Martin et al. 1951, Terres 1980.

Verdin

Auriparus flaviceps



L 3½"

RANGE: Resident from northeastern Baja California, southern California, southern Nevada, northern Arizona, southwestern Utah, central New Mexico, and central Texas south into Mexico. Casually in southwestern California and southwestern Oklahoma.

STATUS: Common.

HABITAT: Inhabits brushy valleys, oak slopes, and other semiarid habitats where there are stiff-twigged and thorny bushes, or trees such as mesquite, hackberry, hawthorn, catclaw, screw bean, paloverde, and cholla.

NEST: Builds a nest that is an oval or ball-shaped mass, up to 8 inches in diameter, of thorny twigs anchored to a limb of almost any tree or shrub species found within its range. Also builds roosting or winter nests.

FOOD: Eats mostly insects, searching among terminal twigs, buds, and under leaves for insects, their eggs and larvae. Also eats spiders; pulp from seed pods of paloverde, mesquite, and ironwood; and fruits of wolf berry and date palm.

REFERENCES: Johnsgard 1979, Taylor 1971, Terres 1980, Whitaker 1943.

Bushtit

Psaltiriparus minimus



RANGE: Resident from extreme southwestern British Columbia, western Washington, western and southern Oregon, southwestern Idaho, northern Nevada, north-central Utah, southwestern Wyoming, north-central Colorado, western Oklahoma, and central Texas south to Baja California, central and southeastern Arizona, and Mexico.

STATUS: Locally common.

HABITAT: Found most frequently in pinyon-juniper habitats, but also occurs in tall sagebrush, mountain-mahogany, chaparral, brushy or tree-lined river banks, and in hillside aspen groves.

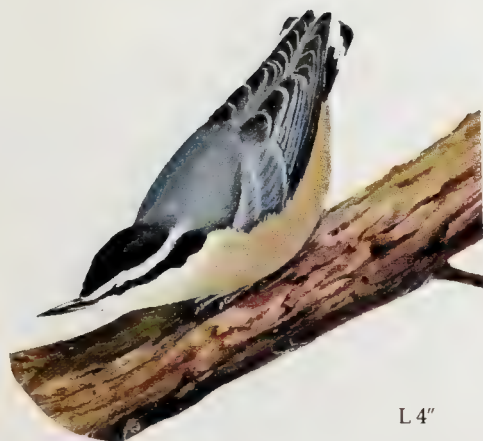
NEST: Builds a gourd-shaped nest of twigs, mosses, roots, lichens, oak leaves, and flowers, that is hung from a branch in a clump of leaves.

FOOD: Gleans insects and spiders from foliage of trees and shrubs; also eats some fruit.

REFERENCES: Addicott 1938, Johnsgard 1979, Terres 1980.

Red-breasted Nuthatch

Sitta canadensis



L 4"

RANGE: Breeds from south-coastal and southeastern Alaska, southern Yukon, central Manitoba, and Newfoundland south to southern California, central and southeastern Arizona, central Colorado, Wyoming, southwestern North Dakota, southern Manitoba, southern Michigan, and north-central Ohio; in the Appalachian Mountains to eastern Tennessee and western North Carolina; and south to southeastern Pennsylvania, southern New Jersey, and southern New York. Winters throughout most of the breeding range except at the higher latitudes and elevations, irregularly south to Baja California, southern Arizona, southern Texas, and central Florida.

STATUS: Common.

HABITAT: Prefers coniferous forests, but sometimes occurs in mixed and deciduous woodlands.

SPECIAL HABITAT REQUIREMENTS: Cavities in trees with a minimum dbh of 12 inches for nest sites, or soft dead wood for cavity excavation.

NEST: Generally uses natural cavities or woodpecker holes for nesting, but can excavate its own cavity in rotted stubs or dead branches. Typically locates nest 15 feet above the ground, but sometimes from 5 to 40 feet. Smears pitch below or around the entrance hole, even when the nest is in a deciduous tree or nest box.

FOOD: Pries open conifer cone scales and removes seeds for much of its food. Also feeds on spiders and some insects.

REFERENCES: Bent 1948, deKiriline 1952, Forbush and May 1955, Terres 1980, Thomas et al. 1979.

White-breasted Nuthatch

Sitta carolinensis



L 5"

RANGE: Resident from northwestern Washington, southern British Columbia, central Montana, southern Manitoba, northern Minnesota, northern Michigan, New Brunswick, and Nova Scotia south to Baja California, southern Nevada, central and southeastern Arizona, the highlands of Mexico, western and east-central Texas, and northern Florida. Absent from most of the Great Plains.

STATUS: Common.

HABITAT: Occurs primarily in deciduous and mixed forests, and locally in coniferous forests. Prefers open woodlands, pinyon-juniper, forest edges, parks, and partly open situations with scattered trees.

SPECIAL HABITAT REQUIREMENTS: Natural tree cavities for nesting, preferably in trees with a minimum of 12 inches dbh.

NEST: Prefers natural cavities in living trees at almost any height for nesting, but will use cavities in dead or dying trees or old woodpecker holes. Rarely, if ever, excavates its own cavity. Chooses apple, elm, maple, aspen, and ponderosa pine for nest trees.

FOOD: Gleans insects from the bark of tree trunks and limbs, but also searches for seeds on the ground. In fall and winter, primarily eats mast, sunflower seeds, and corn. During spring and summer, eats a myriad of arthropods.

REFERENCES: Bailey and Niedrach 1965, Bent 1948, DeGraff et al. 1980, Forbush and May 1955, Kilham 1968, Scott and Patton 1975, Thomas et al. 1979.

Pygmy Nuthatch

Sitta pygmaea



L 3½"

RANGE: Resident from southern interior British Columbia, northern Idaho, western Montana, central Wyoming, and southwestern South Dakota south to Baja California, Mexico, southern Nevada, central and southeastern Arizona, central New Mexico, western Texas, and western Oklahoma.

STATUS: Common.

HABITAT: Generally associated with pine forests; prefers open, parklike forests, especially among ponderosa pines in the lower coniferous forest zone. Occurs less frequently in pinyon-juniper and pines of the Pacific Coast.

SPECIAL HABITAT REQUIREMENTS: Pine forests with dead trees for cavity nest sites.

NEST: Usually excavates nest cavity near the top of a dead pine where the wood is well rotted, or in the underside of a dead branch about 5 to 60 feet above the ground, often at least 25 feet up. Occasionally nests in aspen snags.

FOOD: Searches for food in the tops of pine trees, consuming many insects and conifer seeds. Consumes a diet of about 80 percent insects and spiders.

REFERENCES: Bent 1948, Grinnell and Miller 1944, Johnsgard 1979, Norris 1958, Phillips et al. 1964, Scott et al. 1977.

Brown-headed Nuthatch

Sitta pusilla



L 3½"

RANGE: Resident from southeastern Oklahoma, central Arkansas, the northern portions of the Gulf States, northern Georgia, eastern Tennessee, western North Carolina, south-central and eastern Virginia, southern Maryland, and southern Delaware south to eastern Texas, the Gulf Coast, and southern Florida.

STATUS: Locally common to rare in parts of its range.

HABITAT: Prefers open pine or pine-hardwood woodlands, particularly burned-over areas or clearings where there are dead trees or old stumps. Virtually never found outside the coastal plain of the Southeast, or pine habitats.

SPECIAL HABITAT REQUIREMENTS: Dead trees or stumps for nest excavation.

NEST: Excavates nest cavities in dead trees and stumps (often fire-blackened) or in posts or poles. Cavities are seldom over 13 feet high and usually less than 5 feet above the ground. Occasionally uses old woodpecker holes or natural cavities.

FOOD: Eats mainly insects in summer, foraging for food on tree branches and trunks. Mostly eats pine seeds in winter.

REFERENCES: Bent 1948, Norris 1958, Pearson 1936, Terres 1980.

Brown Creeper

Certhia americana



L 4¾"

RANGE: Breeds from southwestern, central, and southeastern Alaska, central Alberta, central Manitoba, and Newfoundland south to southern California, across to extreme western Texas, southeastern Nebraska, southeastern Missouri, southern Ontario, eastern Ohio, and West Virginia; in the Appalachians to eastern Tennessee and western North Carolina; and to the lowlands of Virginia, Maryland and Delaware. Breeds also through Mexico into Central America. Winters generally through the breeding range, withdrawing from the higher latitudes and elevations and south throughout the eastern United States and southern Texas, the Gulf Coast, and central Florida.

STATUS: Inconspicuous, but locally common.

HABITAT: Inhabits dense coniferous, deciduous, and mixed woodlands, montane forests, and wooded swamps with standing dead trees with loose bark. During migration and in winter, occurs in open woodlands, scrub forests, parks, and suburban trees.

SPECIAL HABITAT REQUIREMENTS: Dead trees with loose bark, preferably with a minimum dbh of 10 inches.

NEST: Constructs nest between loose bark and the trunk of a live, dead, or dying tree, generally 5 to 15 feet above the ground. Occasionally nests in natural cavities or old woodpecker holes.

FOOD: Explores tree trunks and branches for insects and larvae. Also eats a small amount of mast.

REFERENCES: Bent 1948, Davis 1978, DeGraff et al. 1980, Johnsgard 1979, Terres 1980, Thomas et al. 1979.

Red-whiskered Bulbul

Pycnonotus jocosus



L 7"

RANGE: Introduced in 1960 and established in Dade County, southern Florida. Native to India and southern China.

STATUS: Locally common; there are no apparent ecological factors to hinder the spread of this species along coastal, tropical, southeastern Florida.

HABITAT: Has adapted well to exotic trees and shrubs in large suburban yards around Kendall, Florida. Generally stays under cover of vegetation, but occasionally perches in the open. Flocks together in the nonbreeding season and begins roosting assemblages in July and August.

SPECIAL HABITAT REQUIREMENTS: Ornamental trees and shrubs old enough to bear berries and fruits for food.

NEST: Currently nests only within suburbs, using virtually any shrub, hedge, or small tree. Builds nest in the crotch of a low shrub or small tree 2 to 8 feet above the ground.

FOOD: Eats fruits, berries, flowers, nectar, and some insects. The fruit of the Brazil peppertree is a very important food item during winter months.

REFERENCES: Carleton and Owre 1975, Fisk 1966, Sykes in Farrand 1983b.

Cactus Wren

Campylorhynchus brunneicapillus



L 6½"

RANGE: Resident from southern California, southern Nevada, southwestern Utah, and central Arizona to central and southern Texas south to Mexico.

STATUS: Common.

HABITAT: Inhabits southwestern deserts, primarily where there are abundant cacti and thorny trees, especially large cholla, mesquite, and paloverde. Also frequents riparian brush and trees in towns of arid regions.

SPECIAL HABITAT REQUIREMENTS: Thorny shrubs or trees for nesting sites.

NEST: Usually constructs a conspicuous nest in cholla cactus, catclaw, or other thorny shrubs or trees, from 3 to 14 feet, but typically 4 to 9 feet, above the ground. Occasionally may nest in orange trees, old woodpecker holes, or in a hollow cornice of a building. Covered roosting nests are built for use throughout the year.

FOOD: Feeds mostly on the ground, but also gleans insects from branches of trees and shrubs. Consumes insects, some spiders, occasionally lizards and tree frogs, cactus fruit, berries, and some seeds.

REFERENCES: Anderson and Anderson 1959, 1973, Phillips et al. 1964, Terres 1980, Terrill in Farrand 1983b.

Rock Wren

Salpinctes obsoletus



RANGE: Breeds from south-central British Columbia and southern Alberta to the western Dakotas south (east of the coast ranges in Washington, Oregon and northern California) to Baja California and Central America, and east to western Nebraska and central and southern Texas. Winters from northern California, southern Nevada, and southern Utah to north-central Texas south through the southern portions of the breeding range, wandering to lower elevations.

STATUS: Fairly common.

HABITAT: Primarily inhabits arid and semiarid environments, preferring open, rocky areas such as rock outcrops, canyons, fractured cliff faces, talus slopes, and dry earth banks. May be found up to 10,000 feet in the Rocky Mountains and shows no preference for areas with water throughout its range.

SPECIAL HABITAT REQUIREMENTS: Rough, rocky surfaces with crevices for foraging and cover.

NEST: Typically locates nest on slopes of loose rocks and boulders, in crevices of canyon walls, or sometimes in rodent cavities in banks or in tree holes. Builds a well hidden nest, often with a small runway of stones, sometimes 8 to 10 inches long, leading to the nest.

FOOD: Forages almost exclusively in open or relatively unvegetated sites. Gleans insects and spiders from boulders, rocks, barren ground, and crevices.

REFERENCES: Bent 1948, Johnsgard 1979, Verner and Boss 1980, Webster in Farrand 1983b.

Canyon Wren

Catherpes mexicanus



L 4½"

RANGE: Resident from southern interior British Columbia and eastern Washington to Wyoming, southeastern Montana, and southwestern South Dakota south to Baja California and Mexico.

STATUS: Fairly common.

HABITAT: Found in two primary habitats; areas with water, such as boulder-strewn streams, rocky canyons, and river gorges, and major rock formations, such as tall cliffs, large caves, mesas, and buttes. Prefers cool, shaded canyons with rock outcrops.

SPECIAL HABITAT REQUIREMENTS: Small cliffs, talus, or rock outcrops for nesting and foraging.

NEST: Favors ledges in caverns or rocky crevices for nest sites but sometimes attaches nest to a rock face in a cave or wide crevice. May also nest in buildings.

FOOD: Forages mainly in secluded or covered habitats, gleaning insects and spiders from rock surfaces or the ground.

REFERENCES: Bent 1948, Johnsgard 1979, Verner and Boss 1980, Webster in Farrand 1983b.

Carolina Wren

Thryothorus ludovicianus



L 4 3/4"

RANGE: Resident from eastern Nebraska, Iowa, and southeastern Minnesota across to southern Ontario, extreme southwestern Quebec, and southern New England, south to Mexico, the Gulf Coast, and Florida.

STATUS: Common; populations are beginning to recover in the northern portion of its range where they had previously declined.

HABITAT: Found in a variety of habitats from lowland streambank tangles to upland brushy slopes and woodland edges, especially in moist areas with thickets and undergrowth such as honeysuckle, greenbrier, and brush piles. Also frequents cutover forests, cultivated areas with brush heaps or old buildings, and suburban parks and gardens. In winter, moves to low, flat ground near tidewater creeks in the Northeast, and to narrow valleys and deep ravines in other areas.

SPECIAL HABITAT REQUIREMENTS: Low, brushy vegetation.

NEST: Prefers nest sites that are fairly well enclosed. Typically nests in natural tree cavities, woodpecker holes, overturned root cavities, bird-houses, under rocks, and in building crevices. Locates nest usually less than 10 feet above the ground, sometimes in low shrubs or in grasses.

FOOD: Consumes a diet that is about 94 percent animal food, nearly all insects gleaned from trees, shrubs, and the ground. Also eats some snails, lizards, tree frogs, berries, and seeds. Will come to bird feeders for food.

REFERENCES: Armistead in Farrand 1983b, Bent 1948, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Nice and Thomas 1948, Scott et al. 1977, Tate and Tate 1982.

Bewick's Wren

Thryomanes bewickii



L 4½"

RANGE: Breeds from southwestern British Columbia, southern Wyoming, eastern Nebraska, southeastern Minnesota, southern Ontario, and southeastern New York south to Mexico, central Texas, the northern portions of the Gulf States, central Georgia and central South Carolina. Resident in the West; winters from the northern limits of the breeding range, southern Kansas, the lower Ohio Valley, and North Carolina to Mexico, the Gulf Coast, and central Florida.

STATUS: Scarce and local throughout the eastern portion of the breeding range, locally common in the West.

HABITAT: Generally associated with dense, brushy habitats such as thickets of mesquite, oaks, and cacti; chaparral; mixtures of pine, junipers, and oaks; dense growths of alder, cottonwood, and willow. In the Southwest, occurs in mountain canyons up to 6,000 feet in elevation.

SPECIAL HABITAT REQUIREMENTS: A brushy understory and cavities for nesting.

NEST: Nests near the ground in secluded natural tree cavities, old woodpecker holes, rock crevices, deserted buildings, birdhouses, or in almost any cavity where a nest could be built. (Nest and nesting sites are like those of the house wren, and the two species usually compete when in the same area.)

FOOD: Gleans small insects and spiders (about 97 percent of diet) from low trunks and branches of trees and brush, usually under dense cover.

REFERENCES: Beal 1907, Bent 1948, Johnsgard 1979, Miller 1941, Tate and Tate 1982, Verner and Boss 1980.

House Wren

Troglodytes aedon



L 4¼"

RANGE: Breeds from southern and east-central British Columbia and northern Alberta east to southwestern Quebec and New Brunswick, and south to Baja California, Mexico, western and northern Texas, central Arkansas, southern Tennessee, and North Carolina. Winters from southern California to northern Texas, the northern portion of the Gulf States, and coastal Maryland south to Mexico, the Gulf Coast, and Florida.

STATUS: Common.

HABITAT: Originally associated with deciduous forests and open woods, it has adapted to woody vegetation in cities, towns, and around farms. Frequents edges of woodlands, open forests, clearings, swampy woodlands, orchards, farmlands, and suburban gardens. Ranges from the plains up to near timberline in the West but avoids high elevations in the East.

SPECIAL HABITAT REQUIREMENTS: Woody vegetation and cavities for nesting.

NEST: Uses almost any type of cavity as a nest site, including natural cavities in trees, fenceposts, or stumps, woodpecker holes, and bird-houses or other artificial cavities with openings preferably about 1 inch in diameter. Typically chooses a nest site less than 10 feet above the ground.

FOOD: Gleans and hawks insects, which form 98 percent of its diet.

REFERENCES: Bent 1948, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Kendeigh 1941.

Winter Wren

Troglodytes troglodytes



L 3¼"

RANGE: Breeds from coastal southern and southeastern Alaska and northern British Columbia to central Quebec and southern Labrador, south to central California, central Idaho, southeastern Manitoba, southern Wisconsin, and southeastern New York, and in the Appalachians to northeastern Georgia. Winters from southern Alaska and British Columbia east to northeast Colorado, central Iowa, southern Michigan, and Massachusetts south to southern California, southern Texas, the Gulf Coast, and central Florida.

STATUS: Generally uncommon.

HABITAT: Primarily inhabits dense undergrowth of coniferous forests, generally near water. Favors spruce and fir forests, but sometimes inhabits dense mixed and hardwood forests. Frequents thickets near woodland streams, boreal swamps and bogs, banks of marshy ditches, and slash piles. In winter, prefers coniferous and deciduous woodlands with a dense understory, especially in moist areas.

SPECIAL HABITAT REQUIREMENTS: Moist coniferous woodlands with low woody vegetation, or low-lying cold bogs or swamps.

NEST: Usually nests under an upturned root of a tree or under a stump, in a hollow log, brush heap or rocky crevice, or rarely in an old woodpecker hole. Does not typically build its nest in an enclosed cavity as other wrens do.

FOOD: Insects and spiders gleaned from the ground form almost the entire diet.

REFERENCES: Bent 1948, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979.

Sedge Wren

Cistothorus platensis

(formerly Short-billed Marsh Wren)



L 3¾"

RANGE: Breeds from extreme east-central Alberta and central Saskatchewan east to northern Michigan and southern New Brunswick, south to east-central Arkansas, central Kentucky, and southeastern Virginia, and west to central North Dakota and eastern Kansas. Winters from western Tennessee and Maryland to northeastern Mexico, Texas, the Gulf Coast, and Florida.

STATUS: Scarce and local; populations are declining in the Northeast and Midwest.

HABITAT: Inhabits wet meadows and the damp upper margins of marshes and sphagnum bogs. In the Northeast, commonly inhabits sedge meadows, shallow sedge marshes with scattered shrubs and little or no standing water, and coastal brackish marshes of marsh hay cord-grass with scattered low shrubs and herbs. In the Midwest, prefers wet meadows dominated by sedges, cottongrass, mannagrass, and reed grass, but also frequents emergent vegetation associated with marshes, and retired croplands and fields.

SPECIAL HABITAT REQUIREMENTS: Wet meadows or drier edges of marshes for nesting.

NEST: May be loosely colonial in good habitat, otherwise nests singly. Builds nest over land or water in dense vegetation such as canarygrass, sedges, or bulrushes, but shuns cattails; usually places nest 1 to 3 feet above the substrate. Males build many unlined dummy nests, but few are used by females.

FOOD: Gleans insects and spiders from the ground and surrounding marsh vegetation.

REFERENCES: Crawford 1977, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Mousley 1934b, Tate and Tate 1982, Vickery in Farrand 1983b, Walkinshaw 1935.

Marsh Wren

Cistothorus palustris

(formerly Long-billed Marsh Wren)

L 4"



RANGE: Breeds from southwestern and east-central British Columbia and northern Alberta east to northern Michigan and eastern New Brunswick, south to Baja California, southwestern Arizona, extreme western and southern Texas, the Gulf Coast, and east-central Florida. Generally very local in interior North America. Winters in coastal areas throughout the breeding range, and in the interior from the southern United States to Mexico.

STATUS: Locally common.

HABITAT: Prefers large fresh or brackish marshes with an abundance of tall emergent vegetation such as cattails, loosestrife, sedges, or rushes. Also frequents prairie sloughs, pond and sluggish river shores, marsh-fringed lakes, and the banks of tidal rivers bordered with tall emergent vegetation. Prefers large marshes grown with narrow-leaved cattails to those with broad-leaved cattails.

SPECIAL HABITAT REQUIREMENTS: Marshy habitats with tall emergent vegetation.

NEST: Builds domed elliptical nest preferably in cattail stands of moderate density, 3 to 5 feet above the marsh substrate, which is generally shallow water. Usually attaches to cattails or other tall emergent vegetation, but may place it in small bushes or trees. Constructs many dummy nests and uses some for roosting.

FOOD: Gleans insects and spiders from surrounding marsh vegetation and the surface of the water; also hawks for insects and eats a few snails.

REFERENCES: Bent 1948, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Low and Mansell 1983, Verner 1965, Verner and Engelsen 1970, Vickery in Farrand 1983b, Welter 1935.

American Dipper

Cinclus mexicanus
(formerly Dipper)



L 5¼"

RANGE: Resident from western and northeastern Alaska and north-central Yukon to southwestern Alberta, north-central Montana, and southwestern South Dakota south to southern California, north-central and southeastern Arizona, southern New Mexico, Mexico, and Central Mexico.

STATUS: Fairly common.

HABITAT: Found along rapidly flowing mountain streams in the West, with numerous falls and cascades, and beds filled with large rocks and boulders. Primarily in the vicinity of coniferous forests from 2,000 feet to timberline; less frequently found in the vicinity of mountain ponds and lakes.

SPECIAL HABITAT REQUIREMENTS: Clear, permanent streams or rivers.

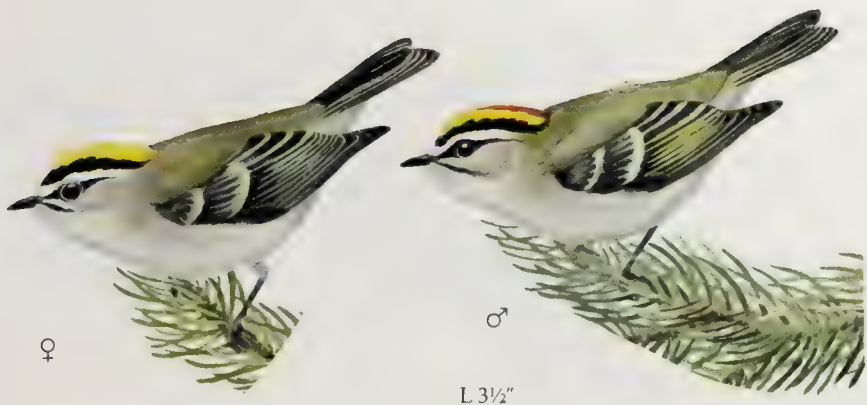
NEST: Usually locates nest over water, either under overhanging rock ledges or under bridges, from just above water level to 15 feet high. Places nest on a rock in midstream, behind a waterfall, or more commonly, in a niche in a rock wall, or sometimes among the roots of a fallen tree.

FOOD: Eats mainly insect larvae and adults, snails, and fish fry. Searches for food while completely submerged under fast-flowing water. Catches some insects in the air by hawking.

REFERENCES: Bakus 1959, Hann 1950, Johnsgard 1979, Thut 1970.

Golden-crowned Kinglet

Regulus satrapa



RANGE: Breeds from southern Alaska to northern Alberta, southern Quebec, and Newfoundland south in the coastal and interior mountains to southern and eastern California, southern Utah, south-central New Mexico, Mexico, Guatemala, and east of the Rockies to southern Manitoba, north-central Michigan, New York, eastern Tennessee, western North Carolina, northern New Jersey, and southern Maine. Winters from south-coastal Alaska and southern Canada south to northern Baja California, through the breeding range to Guatemala, the Gulf Coast, and central Florida.

STATUS: Common in parts of its range; has declined in western regions.

HABITAT: Breeds primarily in dense coniferous forests, especially where spruce is present. Winters in coniferous forests and occasionally in deciduous woodland scrub and brush.

NEST: Builds a globular nest with entrance at the top, woven into the twigs of a horizontal limb of a conifer.

FOOD: Forages over leaves, branches, and trunks, feeding almost entirely on insects and their eggs (bark beetles, scale insects) and especially plant lice. In summer, feeds mainly on flying insects.

REFERENCES: Bent 1949, DeGraff et al. 1980, Forbush and May 1955, Tate and Tate 1982, Terres 1980.

Ruby-crowned Kinglet

Regulus calendula



RANGE: Breeds from northwestern and north-central Alaska, northern Saskatchewan, northern Ontario, and Newfoundland south to southern Alaska, in the mountains to southern California, southern Arizona, south-central New Mexico, and east-central Colorado, and east of the Rockies to central Alberta, southern Manitoba, northeastern Minnesota, northern Michigan, northern New York, northern Maine, and Nova Scotia. Winters from southern British Columbia, Idaho, northern Arizona, Nebraska, southern Ontario, and New Jersey south to Baja California, southern Texas, southern Florida, and through Mexico to Guatemala.

STATUS: Locally common.

HABITAT: Generally inhabits coniferous forests or coniferous-deciduous woodlands during the summer breeding season. In migration and during winter also found in deciduous forests, open woodlands, brush, and scrub.

NEST: Usually attaches nest to pendent twigs beneath a horizontal spruce branch (occasionally fir or pine), generally from 15 to 60 feet above the ground.

FOOD: Gleans or hawks its food, which consists mainly of insects and spiders. Also eats some elderberries and weed seeds.

REFERENCES: Beal and McAtee 1912, DeGraff et al. 1980, Forbush and May 1955, Terres 1980.

Blue-gray Gnatcatcher

Polioptila caerulea



RANGE: Breeds from southern Oregon, northern California, southern Idaho, central Utah, Colorado, Nebraska, western Iowa, southeastern Minnesota, Michigan, southwestern Quebec, central New York, central Vermont and southern Maine south to Baja California, to southeastern Texas, the Gulf Coast, and southern Florida, throughout Mexico to Central America. Winters from southern California, southern Nevada, western and central Arizona, central Texas, the southern portions of the Gulf States, and on the Atlantic Coast from Virginia south through Mexico to Central America.

STATUS: Common in parts of its range, but numbers fluctuate.

HABITAT: In the Southeast, it inhabits forested river bottoms and upland pine woods with an understory of oaks. In other areas, it may inhabit open scrub and woodlands, or tall trees of closed canopy along river flood plains. Throughout the West it breeds in oaks, pinyon-juniper, and less frequently in chaparral.

SPECIAL HABITAT REQUIREMENTS: An abundant supply of arthropods.

NEST: Places nest saddled on a horizontal limb 4 to 70 feet high (average 25 feet), in a conifer or deciduous tree, but usually in deciduous oaks.

FOOD: Gleans food from the tips of branches, leaf surfaces, and bark; also hawks flying insects from perches. Mostly eats arthropods, principally insects, and some spiders.

REFERENCES: Forbush and May 1955, Root 1967, 1969, Terres 1980.

Black-tailed Gnatcatcher

Polioptila melanura



RANGE: Resident from southwestern California and northwestern Baja California south locally to southern Baja California and from northwestern Baja California, southeastern California, southern Nevada, western and central Arizona, southern New Mexico, and western and southern Texas south into Mexico.

STATUS: Common, but may be declining. Listed on the blue list for declining species in 1982.

HABITAT: Found in the lower elevations of the Southwest, where it prefers desert brush and scrub, especially mesquite and creosote bush, and in coastal sagebrush and thorn forests.

NEST: Places its small, deep cup, invariably low (2-4 feet above ground) in buckthorn, laurel, sumac, sagebrush, cactus, or other desert plant.

FOOD: Gleans insects and some spiders from branches and twigs of shrubs. Also eats small amounts of seeds.

REFERENCES: Harrison 1979, Tate and Tate 1982, Terres 1980, Terrill in Farrand 1983c.

Eastern Bluebird

Sialia sialis

L 5½"



RANGE: Breeds from southern Saskatchewan, southern Quebec, and western Nova Scotia south to southern Texas and southern Florida, and west to the Dakotas, western Kansas, Texas, and southeastern New Mexico; also in southeastern Arizona and through the highlands of Mexico to Central America. Winters from the middle portions of the eastern United States south throughout the breeding range.

STATUS: Population low but stable, many dependent on nest boxes.

HABITAT: Inhabits fields, forest edges, open woodlands, and open country with scattered trees, and in coniferous, deciduous, and riparian woodlands.

SPECIAL HABITAT REQUIREMENTS: Low cavities for nesting and perches for foraging.

NEST: Nests in old woodpecker holes, hollows of decayed trees, crevices of rocks, and hollows in wooden fence posts when available. Many now nest in artificial nest boxes placed in open areas or at the edge of a forest.

FOOD: Catches insects and spiders by flying from a perch to the ground or hawking. Eats fruits and a few seeds during winter.

REFERENCES: Beal 1915a, Forbush and May 1955, Hartshorne 1962, Pearson 1936, Rustad 1972, Tate and Tate 1982, Thomas 1946.

Western Bluebird

Sialia mexicana



RANGE: Resident from southern British Columbia, western and south-central Montana, and north-central Colorado south through the mountains to Baja California, western and southern Nevada, southern Utah, western and southeastern Arizona, central New Mexico, western Texas, and in the highlands of Mexico. Wanders in winter to lowland areas throughout the breeding range, and to islands off California and Baja California.

STATUS: Overall population is low but stable.

HABITAT: Mostly inhabits open ponderosa pine forests of the transition zone but is also found in other open coniferous, deciduous, and mixed forests, partly open country with scattered trees, savannah, and riparian woodlands.

SPECIAL HABITAT REQUIREMENTS: Cavities for nesting and perches for feeding.

NEST: Usually nests in old woodpecker holes, but also uses natural cavities and nest boxes. Prefers to locate nests in rather open forests or at forest edges.

FOOD: Sometimes hawks insects from high perches; otherwise flies to the ground from low perches to catch prey. Mostly eats insects and spiders but also some fruits such as elderberries and mistletoe berries.

REFERENCES: Beal 1915a, Herlugson 1982, Tate and Tate 1982.

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Mountain Bluebird

Sialia currucoides

♂



RANGE: Breeds from east-central Alaska, southern Yukon, and western Manitoba south in the mountains to southern California, central and southeastern Nevada, northern and east-central Arizona, and southern New Mexico, and east to northeastern North Dakota, western South Dakota, and central Oklahoma. Winters from southern British Columbia and western Montana south to Baja California, Mexico, and southern Texas, and east to eastern Kansas, western Oklahoma, and central Texas.

STATUS: Population is low but stable.

HABITAT: Nests in nearly all forest types of the Rocky Mountain region, usually from 7,000 to 11,000 feet in open forests or near forest edges. During migration and in winter, also frequents grasslands, open brushy country, and agricultural lands.

SPECIAL HABITAT REQUIREMENTS: Cavity nests and feeding perches.

NEST: Usually nests in old woodpecker holes or natural cavities in dead trees in open areas or near forest edges. Will also use nest boxes.

FOOD: Hawks from high perches or flies to the ground to catch its prey. Probably more insectivorous than the other bluebirds; nearly 92 percent of the diet is animal material; the small amount of vegetable food includes fruits, hackberry seeds, and cedar berries.

REFERENCES: Beal 1915a, Burleigh 1972, Herlugson 1982, Scott et al. 1977, Tate and Tate 1982.

Townsend's Solitaire

Myadestes townsendi



L 6¾"

RANGE: Breeds from east-central and southeastern Alaska, to west-central Mackenzie south in the mountains to southern California, northern and east-central Arizona, central New Mexico, and northern Mexico, and east to southwestern Alberta, western and southern Montana, southwestern South Dakota and northwestern Nebraska. Winters from southern British Columbia, southern Alberta, Montana, and South Dakota south to Baja California, the southern limit of the breeding range in Mexico, and east to western Missouri, western Oklahoma, and central Texas.

STATUS: Common within parts of its range.

HABITAT: During summer, it is found in montane and subalpine coniferous forests and in thickets and brushy areas adjacent to rocky cliffs up to 12,000 feet in elevation. Winters in open woodland, pinyon-juniper associations, chaparral, desert, and riparian woodlands.

SPECIAL HABITAT REQUIREMENTS: Juniper berries for winter food.

NEST: Builds nest on the ground, partly concealed at the base of a pine or fir, under overhanging banks, or among the roots of a fallen tree.

FOOD: Gleans food from the ground, foliage, and fruiting stems, and hawks for flying insects. Eats insects and spiders during the summer, and mostly juniper berries, along with a few other fruits and seeds, during winter.

REFERENCES: Beal 1915b, Poddar and Lederer 1982, Terres 1980, Verner and Boss 1980.

Veery

Catharus fuscescens

dark race
im.

L 6"

rusty race



RANGE: Breeds from south-central and southeastern British Columbia to New Brunswick and southwestern Newfoundland, south to central Oregon, southern Idaho, northeastern South Dakota, northern Illinois, and northern Ohio, in the mountains through West Virginia, western and central Maryland, eastern Kentucky, western and central Virginia, eastern Tennessee, and western North Carolina to northwestern Georgia, and in the Atlantic region to eastern Pennsylvania, central New Jersey, and the District of Columbia. Also in east-central Arizona. Winters in South America.

STATUS: Common.

HABITAT: Inhabits low, moist, deciduous woods, bottomland forests, wooded swamps, and damp ravines; prefers sapling stands of deciduous second-growth or open woods with fairly dense undergrowth of ferns, shrubs, and trees.

SPECIAL HABITAT REQUIREMENTS: Moist woodlands with understory of low trees or shrubs.

NEST: Builds a bulky nest on or near the ground at the base of a shrub, on a mossy stump, in a clump of weeds, or occasionally in a low shrub or tree.

FOOD: Often forages on the forest floor, turning leaves with bill in search of food; occasionally searches for food in trees. Consumes a diet that is about 57 percent animal and 43 percent vegetable.

REFERENCES: Beal 1915b, DeGraff et al. 1980, Forbush and May 1955, Terres 1980.

Gray-cheeked Thrush

Catharus minimus



RANGE: Breeds from northern Alaska, southern Keewatin, and Newfoundland south to southern Alaska, northwestern British Columbia, northeastern Saskatchewan, eastern New York, Massachusetts, central Vermont, northern New Hampshire, central Maine, and northern Nova Scotia. Winters in South America.

STATUS: Common in portions of its range.

HABITAT: During summer, inhabits coniferous forests (primarily spruce) and tall shrubby areas in taiga. During migration and in winter, also found in deciduous forests and open woodlands. Generally inhabits mountain tops in the Northeast.

SPECIAL HABITAT REQUIREMENTS: Coniferous forests.

NEST: Usually builds its nest in willows, alders, or spruces, from ground level to 20 feet, but usually about 6 feet above ground on divergent branches close to the trunk.

FOOD: Generally gleans food from the ground; eats insects, spiders, earthworms, crayfish, and berries.

REFERENCES: Beal 1915b, DeGraff et al. 1980, Terres 1980.

Swainson's Thrush

Catharus ustulatus



L 6¼"

RANGE: Breeds from western and central Alaska, northern Saskatchewan, central Quebec, and Newfoundland south to southern Alaska, southern and east-central California, central Utah, north-central New Mexico, extreme northern Nebraska, eastern Montana, southern Manitoba, northern Minnesota, southern Ontario, northern Pennsylvania, and southern Maine. Also in eastern West Virginia, western Virginia, and western Maryland. Winters from Mexico south.

STATUS: Rare to locally common.

HABITAT: In summer, inhabits dense coniferous forests (especially spruce) and dense tall shrubbery, or recent clearcuts in low damp areas or near water. In parts of range, prefers aspen-poplar forests and willow or alder thickets, and occasionally breeds in coniferous-deciduous forests. In winter, frequents deciduous forests.

SPECIAL HABITAT REQUIREMENTS: Damp forests or adjacent water.

NEST: Builds a bulky cup nest, usually near the trunk, on a horizontal branch of a conifer 2 to 20 feet above the ground.

FOOD: Gleans food from the forest floor, foliage, and branch surfaces. Also eats insects, spiders, millipedes, and small fruits and berries.

REFERENCES: Beal 1915b, DeGraff et al. 1980, Forbush and May 1955, Terres 1980, Verner and Boss 1980.

Hermit Thrush

Catharus guttatus



RANGE: Breeds from western and central Alaska, northern Saskatchewan, and Newfoundland south to southern Alaska, in the mountains to southern California, southern Nevada, southern New Mexico, and western Texas, and east of the Rockies to central Alberta, central Wisconsin, southern Ontario, central Pennsylvania, western Virginia, western Maryland, southern New York, and in the Black Hills in southwestern South Dakota. Winters from southern British Columbia and the northern United States south to Baja California, Mexico, southern Texas, and southern Florida.

STATUS: Common.

HABITAT: In summer, inhabits coniferous, mixed, and deciduous forests with intermediate to high canopy coverage; responds negatively to intensive tree harvests. During migration and in winter, also inhabits chaparral, riparian woodlands, arid pine-oak associations, and desert scrub.

SPECIAL HABITAT REQUIREMENTS: Relatively undisturbed, rather dense forests.

NEST: Usually builds nest in a depression on the ground, under rock ledges, or under low overhanging limbs. Sometimes locates nests in shrubs or small trees near the ground, especially in the West.

FOOD: Gleans most of its food from the ground. Eats insects, spiders, snails, and earthworms, plus considerable amounts of wild fruits in fall and winter.

REFERENCES: Beal 1915b, DeGraff et al. 1980, Forbush and May 1955, Szaro and Balda 1982, Terres 1980, Verner and Boss 1980.

Wood Thrush

Hylocichla mustelina



L 7"

RANGE: Breeds from southeastern North Dakota, northern Michigan, northern Vermont, southwestern Maine, and Nova Scotia south to east-central Texas, the Gulf Coast and northern Florida, and west to eastern South Dakota, central Kansas, and eastern Oklahoma. Winters from southern Texas south to Central America.

STATUS: Common.

HABITAT: Inhabits cool, mature, lowland deciduous or mixed forests, particularly damp situations and near swamps or water. In New England, also found on wooded slopes; has adapted to gardens and city parks.

SPECIAL HABITAT REQUIREMENTS: Deciduous or mixed forests with tall trees.

NEST: Builds a compact cup nest on a horizontal limb, in a fork of a sapling or tree, or well hidden in dense shrubbery, generally 6 to 50 feet (average 10 feet) above ground.

FOOD: Gleans most of its food from the ground, but occasionally gleans insects from tree foliage. Eats insects, spiders, snails, earthworms, and berries.

REFERENCES: Beal 1915b, Brackbill 1943, DeGraff et al. 1980, Forbush and May 1955, Terres 1980.

American Robin

Turdus migratorius



RANGE: Breeds from western and northern Alaska, southern Keewatin, northern Quebec, Labrador, and Newfoundland south to southern California, central and southeastern Arizona, Mexico, southern Texas, and central Florida. Winters from southern Alaska, the northern United States and Newfoundland south to Baja California, southern Texas, and southern Florida, throughout Mexico to Central America.

STATUS: Abundant.

HABITAT: Found in nearly all habitats from tree limit in sparsely wooded barrens up to 12,000 feet in the mountains of the West, along forest borders, hedges, orchards, gardens, city parks, and in suburban yards.

SPECIAL HABITAT REQUIREMENTS: Mud for nest building.

NEST: Places nest, constructed of mud and vegetation, on almost any substantial support, usually in a fork or on a horizontal branch of a shrub or tree; rarely on the ground.

FOOD: Feeds mostly on the ground, searching for almost any edible substance; but also picks fruits from trees and shrubs. Consumes a diet that is about 42 percent animal and 58 percent vegetable.

REFERENCES: Beal 1915b, Forbush and May 1955, Knupp et al. 1977, Terres 1980, Young 1955.

Varied Thrush

Ixoreus naevius



RANGE: Breeds from western and northern Alaska, and northwestern and western Mackenzie south through central and southern Alaska, southwestern Alberta, northwestern Montana, northern Idaho, Washington, and Oregon to extreme northwestern California. Winters from southern Alaska, southern British Columbia, and northern Idaho south through Washington, Oregon, and California to Baja California.

STATUS: Uncommon.

HABITAT: Favors moist, dense stands of fir near mountain lakes, but also inhabits humid coastal and interior montane coniferous forests. Occasionally found in deciduous forests with a dense understory and in tall shrub stands.

NEST: Builds a bulky nest on a horizontal branch or in a crotch of a tree or shrub, usually 10 to 15 feet above ground.

FOOD: Generally forages for food on the ground, but also gleans food from foliage and fruiting stems. Consumes a variety of vegetable and animal foods including insects, snails, earthworms, acorns, weed seeds, berries, and fruits.

REFERENCES: Beal 1915b, Terres 1980, Verner and Boss 1980.

Wrentit

Chamaea fasciata



RANGE: Resident in coastal areas from northwestern Oregon south to northwestern Baja California, and in interior areas of northern and central California.

STATUS: Common resident in suitable habitat.

HABITAT: Primarily inhabits chaparral but also inhabits other habitats from coastal brushlands up to ponderosa and black oak vegetation types where dense stands of shrubs are present.

SPECIAL HABITAT REQUIREMENTS: Dense shrubs.

NEST: Builds a compact cup nest of coarse bark, plant fibers, and grasses, which it conceals 1 to 4 feet above the ground in shrubs such as *Baccharis*.

FOOD: Gleans food from bark surfaces of shrubs; eats primarily insects, spiders, and small fruits.

REFERENCES: Erickson 1938, Terres 1980, Verner and Boss 1980.

Gray Catbird

Dumetella carolinensis



L 7¾"

RANGE: Breeds from southern British Columbia, southern Ontario, and Nova Scotia, south to central New Mexico and northern Florida, and west to northern and south-central Washington, south-central and eastern Oregon, north-central Utah, and central and northeastern Arizona. Winters from north-central and eastern Texas, the central portions of the Gulf States and in the Atlantic Coastal lowlands from Long Island south along the Gulf-Caribbean slope of Central America.

STATUS: Common in breeding season.

HABITAT: Prefers dense thickets of shrubby edge habitat, but also inhabits shrubs, briars, vines along woodland borders, dry marsh edges, roadside shrubs, old house sites, abandoned fields, and fence rows.

SPECIAL HABITAT REQUIREMENTS: Low, dense, shrubby vegetation.

NEST: Hides nest about 3 to 10 feet above the ground in almost any dense woody vegetation such as multiflora rose, barberry, lilac, mock-orange, osage orange, a hedge, or conifer tree.

FOOD: Gleans food from the ground; about half of diet is insects. In the fall, eats a variety of fruits.

REFERENCES: Forbush and May 1955, DeGraff et al. 1980, Nickell 1965, Terres 1980.

Northern Mockingbird

Mimus polyglottos
(formerly Mockingbird)



RANGE: Resident in scattered localities across southernmost Canada from Alberta to Newfoundland; generally resident from northern California, northern Utah, and southern North Dakota, east to southern Maine and south into Mexico. Some northern birds move southward in winter.

STATUS: Common.

HABITAT: Inhabits a variety of open to partly open landscapes such as farm hedges, isolated shrub patches and trees of the prairie, orchards, woodland edges, pastures with scattered fruit-bearing shrubs, and suburbs and cities; absent from forest interiors.

SPECIAL HABITAT REQUIREMENTS: Low, dense, woody vegetation, elevated perches, and a variety of persistent edible fruits.

NEST: Builds nest in a fork or on a limb of a small tree, shrub, or vine (preferably evergreen), typically 3 to 10 feet above the ground. Usually produces two broods each year; builds a new nest for each brood.

FOOD: Gleans insects from the ground and foliage, or hawks from the air. Eats fruits in fall and winter.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Laskey 1962, Terres 1980, Verner and Boss 1980.

Sage Thrasher

Oreoscoptes montanus



RANGE: Breeds largely between the Sierra Nevada-Cascade Mountain axis and the Rocky Mountains from southern British Columbia, Montana, and Wyoming south to east-central California, southern Nevada, northern Arizona, New Mexico, and northwestern Texas. Winters from northern Arizona and central Texas south to northern Mexico.

STATUS: Common throughout most its range.

HABITAT: Mainly limited to semiarid sagebrush plains, but may extend into junipers and mountain-mahogany habitats near sagebrush.

SPECIAL HABITAT REQUIREMENTS: Sagebrush.

NEST: Sometimes nests on the ground under sagebrush, but usually in branches near the main stem of sagebrush plants, 1 to 3 feet above ground. May also nest in other low-growing shrubs such as greasewood, horsebrush, rabbitbrush, and saltbush.

FOOD: Gleans food from the ground, including great numbers of grasshoppers, Mormon crickets, and other insects. Also eats fruits and berries in the fall.

REFERENCES: Reynolds 1981, Reynolds and Rich 1978, Rich 1978, Terres 1980, Webster in Farrand 1983c.

Brown Thrasher

Toxostoma rufum



L 10"

RANGE: Breeds from southeastern Alberta east to New England and south to Colorado, northern and eastern Texas, the Gulf Coast, and southern Florida. Winters in the south from Texas eastward, ranging north in the Mississippi Valley to Illinois and along the Atlantic Coast to Massachusetts. Rare visitor as far west as the Pacific Coast in migration and winter.

STATUS: Common in parts of its range.

HABITAT: During summer, inhabits dry thickets in wooded and farming country, brushy pastures, second-growth woods, fencerows, brier patches, roadsides, and sometimes shrubbery of gardens.

SPECIAL HABITAT REQUIREMENTS: Low, dense, woody vegetation for nesting and cover.

NEST: Builds a bulky nest in any of a variety of shrubs (usually thorny) or low trees, up to 14 feet from the ground, but sometimes on the ground under a small shrub.

FOOD: Gleans food from the ground or in shrubs. In spring, eats almost entirely insects, spiders and worms; in summer and fall, eats mostly fruits, mast (mainly acorns), and waste corn.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Kaufman in Farrand 1983c, Terres 1980.

Long-billed Thrasher

Toxostoma longirostre



L 10"

RANGE: Resident in southern Texas and eastern Mexico. Accidental in western Texas.

STATUS: Abundant within its range.

HABITAT: Inhabits the brush country of southern Texas, especially dense mesquite. Also found among bottomland willow, huisache, condalia, and various other shrubs.

SPECIAL HABITAT REQUIREMENTS: Dense shrubs.

NEST: Nests in pricklypear, yucca, mesquite, or other shrubby plants, usually 4 to 8 feet above the ground, and near the center of the plant.

FOOD: Uncovers food in debris on the ground and in loose soil; mostly eats antlions, ants, beetles, bugs, termites, spiders, and hackberries.

REFERENCES: Cottam and Knappen 1939, Kaufman in Farrand 1983c, Oberholser 1974b, Terres 1980.

Bendire's Thrasher

Toxostoma bendirei



RANGE: Breeds in southeastern California, southern Nevada, southern Utah, western New Mexico, and Sonora. Winters from central-southern Arizona to Sinaloa. Rare in fall to the southern coast of California.

STATUS: Locally common.

HABITAT: Inhabits open desert habitats, especially areas with tall vegetation, cholla cactus, creosote bush, and yucca. May also inhabit pinyon-juniper-sage communities, but tends to avoid large areas of continuous, dense brushy cover and grasslands.

SPECIAL HABITAT REQUIREMENTS: Desert communities.

NEST: Builds a compact nest in almost any of the shrubby vegetation found within its habitat, usually 3 to 10 feet above the ground.

FOOD: Spends much of its time on the ground searching and digging for food. Probably has food habits similar to those of other thrashers.

REFERENCES: Bent 1948, Phillips et al. 1964, Terres 1980, Terrill in Farrand 1983c.

Curve-billed Thrasher

Toxostoma curvirostre



L 10"

RANGE: Resident from central and southeastern Arizona, central and northeastern New Mexico, southeastern Colorado, northwestern Oklahoma, southwestern Kansas, and western and central Texas south to southern Mexico.

STATUS: Common to abundant.

HABITAT: Inhabits deserts with extensive thickets of thorny shrubs (paloverde and mesquite) and dense large cactus (saguaro and cholla), and in brushy riparian and residential areas. Prefers areas with thorny shrubs and thickets at the edge of woodlands.

SPECIAL HABITAT REQUIREMENTS: Desert shrubs.

NEST: Usually builds nest in the fork of cholla cactus but may be in yucca, clumps of mistletoe in mesquite and cottonwood, or in mesquite or similar thickets. Favors nest sites at the edge of woodlands or in cultivated areas.

FOOD: Digs in the soil with its curved bill searching for food, and eats beetles, other insects, seeds of cacti, berries, and other fruit.

REFERENCES: Oberholser 1974b, Terres 1980, Terrill in Farrand 1983c.

California Thrasher

Toxostoma redivivum



RANGE: Resident in California north to Humboldt and Shasta Counties (west of the Cascade Mountains-Sierra Nevada and the deserts), and in northwestern Baja California.

STATUS: Fairly common in suitable habitat.

HABITAT: Found most abundantly along mountain bases and up to 5,000 feet elevation. Prefers slopes covered with chaparral or early tree stages of blue oak savannah, digger pine-oak, and riparian deciduous types; also found in foothill towns with mixed brush and short trees, but avoids areas with dense tree canopies.

SPECIAL HABITAT REQUIREMENTS: Dense shrubs.

NEST: Builds a large, well-concealed loose cup nest near the ground in a large bush or scrubby tree.

FOOD: Digs in the soil and turns over leaves with its bill in search of food. Eats a diet consisting of insects, spiders, seeds of berries, hazelnuts, weed seeds, and small fruits.

REFERENCES: Beal 1907, Terres 1980, Verner and Boss 1980, Webster in Farrand 1983c.

Crissal Thrasher

Toxostoma dorsale

L 10½"



RANGE: Resident from southeastern California, southern Nevada, southwestern Utah, northwestern and central Arizona, central New Mexico, and western Texas south to northeastern Baja California, central Sonora and central Chihuahua.

STATUS: Common.

HABITAT: Inhabits the more heavily vegetated areas of the southern deserts, such as tall brush along rivers and large washes, and dense mesquite or chaparral from sea level to 6,000 feet elevation.

SPECIAL HABITAT REQUIREMENTS: Dense desert shrubs.

NEST: Most commonly builds a nest saddled on a branch or in a fork of mesquite trees, but also in willow, sagebrush, greasewood, or other desert shrubs, usually 2 to 8 feet above the ground.

FOOD: Eats berries, wild grapes, and insects. (Little is known about its food habits.)

REFERENCES: Bent 1948, Phillips et al. 1964, Terres 1980, Webster in Farrand 1983c.

Le Conte's Thrasher

Toxostoma lecontei



RANGE: Resident in the southern San Joaquin Valley of California and across the deserts east of the coast ranges and the Sierra Nevadas to southern Nevada and southwestern Utah, south to Baja California, northern Sonora, and western and south-central Arizona.

STATUS: Uncommon and local.

HABITAT: Lives in the hottest, driest, most barren deserts of the Southwest, and is most abundant in saltbush and open creosotebush deserts.

SPECIAL HABITAT REQUIREMENTS: Deserts with scattered shrubs.

NEST: Builds its nest, a bulky mass of thorny twigs and sticks, usually in cholla cactus but also in other desert shrubs or trees such as mesquite, paloverde, saltbush, sage, ocotillo, and ironwood, usually 4 to 8 feet above the ground.

FOOD: Has food habits that are probably similar to those of other thrashers.

REFERENCES: Bent 1948, Phillips et al. 1964, Terres 1980, Webster in Farrand 1983c.

Water Pipit

Anthus spinoletta



RANGE: Breeds on the Arctic tundra and in the mountains of the West and in Maine. Winters on the Pacific Coast from British Columbia south, and from the southern United States south through Mexico into Central America.

STATUS: Common.

HABITAT: Breeds in alpine and arctic habitats with rough features such as tussocks, tilted rocks, or eroded spots for nest sites. Requires nesting habitat that is free of snow early in the breeding season; prefers moss-grown slopes with southern exposures.

SPECIAL HABITAT REQUIREMENTS: Alpine or arctic tundra with some rough features.

NEST: Builds nest on the ground in the shelter of a rock or bank, beside a mossy hummock, or at the base of a tussock.

FOOD: Forages while walking, gleaning food from the ground and low vegetation. Eats seeds of grasses and weeds, insects, spiders, mites, small mollusks, and crustaceans.

REFERENCES: Forbush and May 1955, Gibb 1956, Sutton and Parmalee 1954a, Terres 1980, Verbeek 1970.

Sprague's Pipit

Anthus spragueii

L 5½"



RANGE: Breeds from north-central Alberta, central Saskatchewan, and west-central and southern Manitoba south to Montana, western South Dakota, North Dakota, and northwestern Minnesota. Winters from the southern tier of the Great Plains States south through Mexico.

STATUS: Common.

HABITAT: Primarily inhabits extensive areas of grasslands dominated by grasses of medium height. Also inhabits large alkaline meadows and meadow zones of large alkali lakes.

SPECIAL HABITAT REQUIREMENTS: Extensive prairie.

NEST: Constructs nest of grasses in hollows of the ground, and in clumps of grasses or grasslike plants.

FOOD: In summer, mostly eats insects and weed seeds. In winter, flocks frequently in weed-grown fields, eating weed seeds.

REFERENCES: Bent 1950, Forbush and May 1955, Johnsgard 1979, Terres 1980.

Bohemian Waxwing

Combycilla garrulus



L 6¼"

RANGE: Breeds from central Alaska, Yukon, southwestern Mackenzie, and northern Manitoba south to northern parts of Washington, Idaho, and Montana, central Saskatchewan, and central Manitoba. Winters south to Washington, Colorado, the Great Lakes, and Maine, east to Ontario, southern Quebec, Nova Scotia, and the northern tier of states. Winters irregularly to California, Arizona, northern New Mexico, and northern Texas.

STATUS: Common.

HABITAT: During summer, inhabits open coniferous forests, muskegs, and less frequently, mixed coniferous-deciduous woodlands. Wanders in large flocks in winter and may be abundant wherever food is available.

NEST: Constructs nest of twigs, grasses, and lichens, usually on a horizontal branch of an isolated spruce, tamarack, or pine in open muskeg, 4 to 50 feet above the ground.

FOOD: In summer, mostly eats insects, catching many of them by hawking from high perches. In fall and winter, eats mostly fruits, with fruits of mountain-ash and berries of cedar and juniper the most important winter foods. In spring, also eats sap from maple trees.

REFERENCES: Bent 1950, Eckert in Farrand 1983c, Forbush and May 1955, Terres 1980.

Cedar Waxwing

Bombycilla cedrorum



L 5¼"

RANGE: Breeds from southeastern Alaska, central British Columbia, Alberta, Saskatchewan, northern Manitoba, Ontario, central Quebec, and Newfoundland south to northern California, Nevada, Utah, Colorado, South Dakota, central Missouri, Illinois, Indiana, northern Georgia, western North Carolina, and Virginia. Winters from southern British Columbia, Montana, Saskatchewan, Manitoba, Ontario, New York, and New England south to Central America.

STATUS: Locally common to rare.

HABITAT: Inhabits a wide variety of open coniferous and deciduous forests, forest edges, farmsteads, parks, and residential areas, but absent from dense forests. During winter, found almost anywhere that trees and shrubs with persistent fruits are present.

SPECIAL HABITAT REQUIREMENTS: Fruit- and berry-producing trees and shrubs.

NEST: Builds its nest semicolonially in dense coniferous thickets (often cedar) but will use a variety of deciduous trees and shrubs. Places nest on a horizontal limb, often in a crotch next to the main trunk, 4 to 50 feet above the ground.

FOOD: Gleans insects from leaf surfaces or hawks from perches. In summer, consumes a diet of about 20 percent insects. In fall and winter, eats nearly all fruits and berries.

REFERENCES: DeGraff et al. 1980, Eckert in Farrand 1983c, Forbush and May 1955, Lea 1942, Putnam 1949, Terres 1980.

Phainopepla

Phainopepla nitens

L 6¼"



RANGE: Breeds from central California, southern Nevada, southern Utah, southern New Mexico, and western Texas south to Baja California and into Mexico. Winters from southern California, southern Nevada, central Arizona, southern New Mexico and western and southern Texas south into Mexico.

STATUS: Locally common to uncommon or rare.

HABITAT: In deserts, primarily inhabits washes, riparian areas, and other habitats that support a brushy growth of mesquite and paloverde. In more northern and coastal areas, inhabits oak chaparral and riparian oak woodlands.

SPECIAL HABITAT REQUIREMENTS: Trees or shrubs and berries (especially mistletoe).

NEST: Builds nest (almost exclusively by the male) in a forked limb of a mesquite, cottonwood, hackberry, willow, sycamore, oak, or citrus tree, often in a clump of mistletoe, 4 to 50 feet above the ground.

FOOD: During the breeding season, captures many insects by hawking from high perches. During other periods, primarily eats fruits and berries (especially mistletoe berries).

REFERENCES: Phillips et al. 1964, Terres 1980, Terrill in Farrand 1983c, Verner and Boss 1980.

Northern Shrike

Lanius excubitor



L 8"

RANGE: Breeds in Alaska, the Yukon, southwestern Mackenzie, and northern parts of Manitoba, Quebec, and Labrador. Winters from southern Alaska and the southern half of Canada south to northern California, central Nevada, northern Arizona, northern New Mexico, Kansas, northern Missouri, central Illinois, Indiana, Ohio, Pennsylvania, and New Jersey.

STATUS: Locally common in summer range; uncommon in winter.

HABITAT: Inhabits a broad belt of coniferous forest or taiga across Canada and Alaska during summer; strongly prefers forest edges, open willow brush, and brush-bordered swamps and bogs. Prefers semiopen country with short grasses and scattered trees or shrubs during winter.

SPECIAL HABITAT REQUIREMENTS: Elevated perches, short vegetation.

NEST: Builds a bulky, loose nest of twigs, in spruces, willows, or bushes, 5 to 20 feet above the ground.

FOOD: Attacks prey from an elevated perch by hawking or hovering, then diving and pouncing. Mostly eats small birds and mammals; also eats insects (especially grasshoppers and crickets), and some snakes, lizards, and frogs.

REFERENCES: Bent 1950, DeGraff et al. 1980, Eckert in Farrand 1983c, Miller 1931, Terres 1980.

Loggerhead Shrike

Lanius ludovicianus



L 7"

RANGE: Breeds from central Alberta, central Saskatchewan, southern Manitoba, Minnesota, central Wisconsin, central Michigan, and south-eastern Ontario, south to Mexico and the Gulf Coast. Very rare or absent from most of the Appalachians, Pennsylvania, New York, and New England. Winters in the southern half of the United States and in Mexico.

STATUS: On the 1982 Blue List for declining species as a species of concern (mostly in the East); common in parts of the West.

HABITAT: Inhabits open country with scattered shrubs or small trees such as shelterbelts, cemeteries, farmsteads, or hedgerows in the plains country and Midwest. In the West, breeds in savannah, pine-oak woodlands, and chaparral types, and prefers very open stands.

NEST: Builds a bulky, cup-shaped nest in a variety of shrubs and low, dense trees, rarely less than 3 feet or more than 25 feet above the ground. Hides the nest well below the crown of the bush or tree.

FOOD: Sometimes hawks for aerial insects, but takes most of its prey as it dives to the ground from an elevated perch. In the West, eats about 83 percent insects; in the East, 68 percent. Eats mostly grasshoppers and crickets, but also a variety of other insects, small mammals, birds, and reptiles.

REFERENCES: Beal and McAtee 1912, Eckert in Farrand 1983c, Johnsgard 1979, Kridelbaugh 1983, Miller 1931, Morrison 1981, Porter et al. 1975, Tate and Tate 1982.

European Starling

Sturnus vulgaris
(formerly Starling)



RANGE: Introduced to North America from Europe. Breeds from southeastern Alaska and the southern half of all Canadian provinces south to Mexico, the Gulf of Mexico, and southern Florida. Still uncommon in some recently occupied parts of the Southwest and the Rocky Mountains, but continues to expand range. Migrates sometimes in the northern part of the range.

STATUS: Abundant in most of its range.

HABITAT: Occupies a great variety of habitats from suburban to rural and woodlands wherever suitable nesting sites occur. Appears to favor thickly settled agricultural areas and tends to avoid dense forests away from human habitation.

SPECIAL HABITAT REQUIREMENTS: Cavities for nesting.

NEST: Normally selects an old woodpecker or natural cavity in trees, utility poles, or fence posts but is extremely adaptable in its choice of nest sites. Usually nests earlier than many other cavity nesters and may be a serious competitor for available nest cavities.

FOOD: Generally forages on the ground. Is sometimes considered a serious agricultural pest in some areas because it eats practically all grains, digs up sprouting seeds, and eats livestock feed. However, is considered beneficial in some areas because more than half of the diet is animal material, including clover weevils, cutworms, and Japanese beetles. Also eats a variety of domestic and wild fruits.

REFERENCES: Forbush and May 1955, Kalmbach 1928, Kessel 1953, 1957, Planck 1967, Royall 1966, Small 1974.

White-eyed Vireo

Vireo griseus



L 4½"

RANGE: Breeds from southeastern Nebraska and central Iowa to southern Michigan, southern Ontario, and southern Massachusetts, south through eastern Texas and Florida into eastern Mexico. Winters from southern Texas south to Central America and east across the Gulf Coast to Florida, north to central coastal North Carolina.

STATUS: Common.

HABITAT: Inhabits deciduous thickets, woodland edges, brambles, undergrowth, hedgerows, and the dense understory of bottomland woodlands, generally favoring thickets near water. May inhabit highlands in the South.

SPECIAL HABITAT REQUIREMENTS: Low shrubby vegetation.

NEST: Builds a cone-shaped cup nest that is suspended from forked twigs of a low shrub or tree, usually well concealed, 1 to 8 feet above the ground.

FOOD: Gleans its food, primarily insects, from branches and leaves. Eats mostly animal matter (90 percent of diet), but eats some berries and small fruits in winter.

REFERENCES: Chapin 1925, Forbush and May 1955, Johnsgard 1979, Nolan and Wooldridge 1962, Sykes in Farrand 1983c.

Bell's Vireo

Vireo bellii



L 4¼"

RANGE: Breeds from southern California (local and rare), southern Nevada, Arizona, southern New Mexico, north into the Midwest (east of the Rocky Mountains) to North Dakota and east to Illinois and south to southwestern Tennessee, Arkansas, northwestern Louisiana, Texas, and Mexico. Winters from Mexico south to Central America.

STATUS: Rare to absent from some former ranges in California, declining in Kansas, Oklahoma, and Texas. (Some decline may result from cowbird parasitism.)

HABITAT: Throughout most its range, inhabits streamside willows. In the arid Southwest, lives along water courses and marshes where mesquite is mixed with cottonwood, saltcedar, elderberry, and desert hackberry. In the Great Plains, generally associated with thickets near streams and rivers, or with second-growth scrub, forest edges, and brush patches.

SPECIAL HABITAT REQUIREMENTS: Dense riparian shrubs.

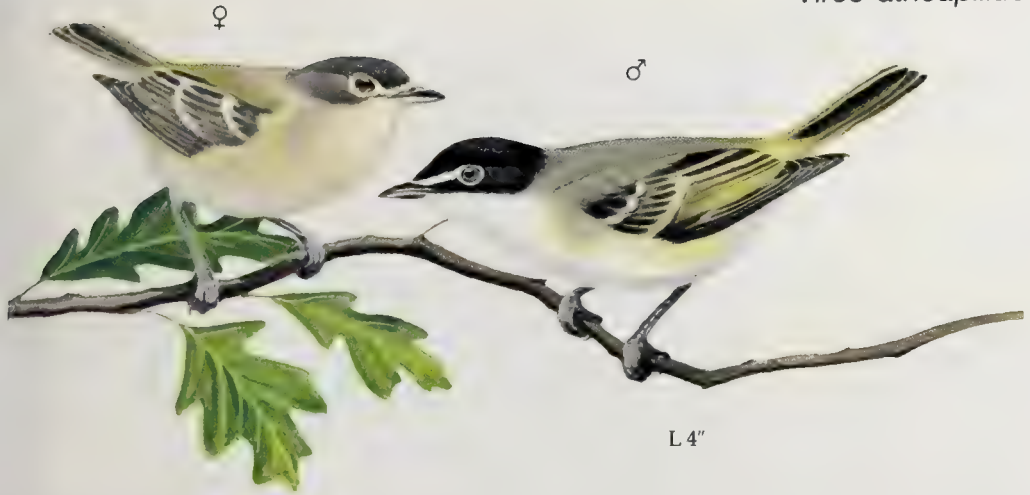
NEST: Builds a small, basketlike cup nest attached to a forked branch of mesquite, hackberry, catclaw, oak, willow, ash, cottonwood, or low shrub, usually near water and seldom more than 5 feet above the ground.

FOOD: Mostly eats animal matter (insects and spiders), gleaned from leaves and branches; also eats a few berries.

REFERENCES: Chapin 1925, Forbush and May 1955, Johnsgard 1979, Tate and Tate 1982, Verner and Boss 1980, Terrill in Farrand 1983c.

Black-capped Vireo

Vireo atricapillus



RANGE: Breeds in central Oklahoma locally through central and western Texas to north-central Mexico. Winters mainly in western Mexico.

STATUS: Fairly common to uncommon. Populations decreasing.

HABITAT: Generally inhabits the dense, low, ragged-topped thickets growing in hot, rocky hillsides, including stands of oaks, mescalbean, sumac, cedar, or other chaparral brush; prefers scrub oaks. May also be found in prairie ravines and early successional stages of brushlands. Prefers habitat arranged in rectangular or oval formation instead of linear.

SPECIAL HABITAT REQUIREMENTS: Low, dense shrubs or trees.

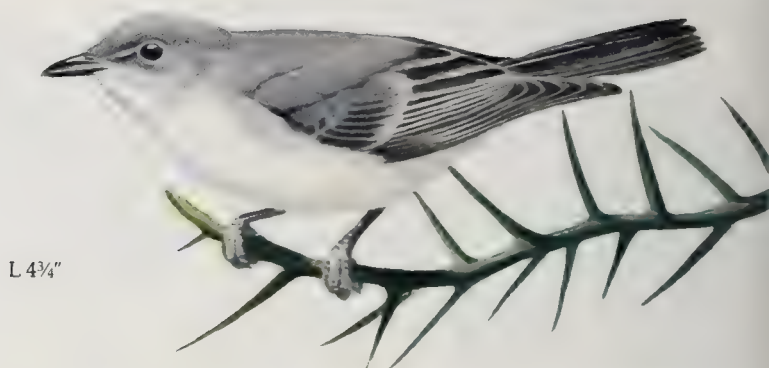
NEST: Builds a deep, cuplike nest suspended from a fork of slender twigs in trees or shrubs, usually 2 to 6 feet above the ground. Prefers oaks in parts of its range, but uses other tree and shrub species.

FOOD: Gleans insects from leaves of shrubs (especially oaks). Also eats a few spiders and small fleshy fruits.

REFERENCES: Graber 1961, Kaufman in Farrand 1983c, Johnsgard 1979, Oberholser 1974b.

Gray Vireo

Vireo vicinior



RANGE: Breeds locally from southern California, southern Nevada, southern Utah, and northwestern and central New Mexico south to Baja California, central and southeastern Arizona, southern New Mexico, western Texas, and central Mexico. Also in western Oklahoma. Winters in southern Arizona, western Texas, and western Mexico.

STATUS: Rare to locally common.

HABITAT: Inhabits thorn scrub, oak-juniper woodland, pinyon-juniper, dry chaparral, mesquite, and riparian willow habitats. Favors dry chaparral that forms a continuous zone of twigs 1 to 5 feet above ground.

SPECIAL HABITAT REQUIREMENTS: Low, dense shrubs.

NEST: Builds a basketlike cup nest that is suspended 3 to 8 feet above the ground from the forks of twigs in a variety of low, thorny shrubs and small trees.

FOOD: Gleans food (mostly insects) from leaves and branches of scrub oaks and other thickets.

REFERENCES: Chapin 1925, Johnsgard 1979, Terres 1980, Terrill in Farrand 1983c.

Solitary Vireo

Vireo solitarius

L 4¾"

Rocky Mt.
race



RANGE: Breeds from central British Columbia east through central Canada to northern Ontario and Newfoundland, southwest of and through the Rockies to southern California and west Texas, south through Mexico to Honduras, and east of the Rockies to North Dakota, Illinois, and Massachusetts; in the Appalachian and Piedmont regions to eastern Tennessee, Alabama, Georgia, South Carolina, North Carolina, Virginia, and Maryland. Winters from southern California, central Texas, the northern portions of the Gulf States and North Carolina south to Costa Rica.

STATUS: Common.

HABITAT: Usually inhabits coniferous or coniferous-deciduous forests, especially spruce and tamarack swamps in parts of its range. Seems to prefer open mixed forests with considerable undergrowth.

NEST: Builds a deep cup nest that is suspended from the fork of a horizontal branch, generally 3 to 20 feet above the ground, often about midway in a small conifer, but occasionally in a small deciduous tree or shrub.

FOOD: Gleans most food from twigs and foliage but occasionally hawks for flying insects. Mostly eats insects, plus a few spiders and small fruits.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Harrison 1975, Johnsgard 1979, Petersen in Farrand 1983c, Terres 1980.

Yellow-throated Vireo

Vireo flavifrons



RANGE: Breeds from southern Manitoba, Minnesota, southern Ontario, New Hampshire and southwestern Maine south to eastern Texas, the Gulf Coast and central Florida and west to the Dakotas, Nebraska, Kansas, Oklahoma, and west-central Texas. Winters mainly in Mexico and Central and South America, but a few winter in Florida.

STATUS: Rather uncommon to common.

HABITAT: Generally associated with mature, moist deciduous forests, especially river bottom forests or north-facing slopes (in southern parts of range), and prefers open woodlands with partially open canopies. Found less frequently in wooded residential areas, seldom in dense deciduous forests, and rarely in coniferous forests.

SPECIAL HABITAT REQUIREMENTS: Open, mature deciduous woodlands.

NEST: Suspends nest between the forks of a slender branch, usually near the trunk, of a deciduous tree, preferably a large oak, normally over 30 feet above the ground (range 3 to 60 feet.)

FOOD: Gleans most of its food from branches and foliage; occasionally hawks for flying insects. Mostly eats insects, spiders, and a few snails, but also a few small fruits and berries.

REFERENCES: Chapin 1925, Forbush and May 1955, James 1976, Johnsgard 1979.

Hutton's Vireo

Vireo huttoni



L 4''

RANGE: Resident from southwestern British Columbia south through western Washington, Oregon, and California to Baja California, and from central Arizona, southwestern New Mexico, and western Texas south to Guatemala.

STATUS: Fairly common.

HABITAT: Primarily inhabits live oak forests but also pine-oak communities; mountain canyons with sycamores, maples, and tall chaparral; or streamside willows. Prefers tree stands with open canopies.

SPECIAL HABITAT REQUIREMENTS: Live oaks.

NEST: Builds a hanging cup nest that is anchored to horizontal twigs and usually near the tips of the branches, mostly in oaks. Locates nest 7 to 25 feet above the ground.

FOOD: Gleans food from foliage and small twigs, and occasionally hawks flying insects. Mostly eats insects, plus some spiders and small berries.

REFERENCES: Chapin 1925, Harrison 1979, Verner and Boss 1980, Terrill in Farrand 1983c.

Warbling Vireo

Vireo gilvus



RANGE: Breeds from southeastern Alaska, northern British Columbia, and southern Mackenzie southeast to southern Ontario and southern New Brunswick, south to northern Mexico, Alabama, and Virginia. Winters mostly in Mexico and Central America.

STATUS: Common and widespread.

HABITAT: Inhabits open deciduous and mixed deciduous-coniferous forests, especially streamside vegetation, but also in groves, scrubby hillside trees, and residential areas. In mixed forests, generally associated with the deciduous trees, and prefers forests with a substantial forb or shrub layer and low to intermediate canopy cover.

SPECIAL HABITAT REQUIREMENTS: Scattered deciduous trees or wooded streamsides.

NEST: Builds a cup nest that is usually suspended from a horizontal branch of a deciduous tree, often poplar or aspen, generally in branches well away from the tree trunk and higher than those of other vireos (20 to 90 feet above the ground).

FOOD: Gleans much of its food from the mid to upper canopy of deciduous trees. Eats mostly animal matter but includes some small fruits.

REFERENCES: Chapin 1925, DeGraff et al. 1980, Forbush and May 1955, Harrison 1975, James 1976, Johnsgard 1979.

Philadelphia Vireo

Vireo philadelphicus



RANGE: Breeds from east-central British Columbia to central Manitoba and southwestern Newfoundland, south to south-central Alberta, north-central North Dakota, northeastern Minnesota, southern Ontario, northern New Hampshire, northern Vermont, and Maine. Winters in Central America.

STATUS: Uncommon to rare.

HABITAT: Inhabits open deciduous, coniferous, or mixed forests, woodland edges, burned or cutover areas with young deciduous regeneration, and willow and alder thickets along streams. Is restricted to aspen groves in parts of its range.

NEST: Builds a deep cup nest that is suspended from a horizontal, forked branch of a deciduous tree or shrub, usually 10 to 40 feet above the ground.

FOOD: Mainly (93 percent) eats animal material (insects and some spiders), most of which is gleaned from foliage and branches; catches some flying insects by hawking. Also eats some wild fruits.

REFERENCES: Chapin 1925, DeGraff et al. 1980, Johnsgard 1979, Petersen in Farrand 1983c.

Red-eyed Vireo

Vireo olivaceus

(includes Yellow-green Vireo (*Vireo flavoviridis*))



L 5"

RANGE: Breeds from southwestern British Columbia and southern Mackenzie southeast to central Ontario and the Maritime Provinces, south to northern Oregon, eastern Colorado, western Oklahoma to central Texas, the Gulf Coast, and central Florida. Very rare in California, Arizona, and southern Texas. Winters in South America.

STATUS: Abundant; rare in the Southwest.

HABITAT: Inhabits open deciduous and mixed forests with dense understory of saplings, in wooded clearings, or borders of burns. Found in both upland and river-bottom forests, and sometimes in residential areas where abundant shade trees provide a continuous canopy. Seldom found where conifers make up 75 percent or more of the basal area.

SPECIAL HABITAT REQUIREMENTS: Deciduous trees with dense understory.

NEST: Builds nest in deciduous or coniferous trees or shrubs. Suspends deep cup nest from a horizontal fork of a slender branch, usually in dense foliage 5 to 10 feet above the ground, but sometimes as high as 60 feet.

FOOD: Consumes insects, gleaned from leaf surfaces in mid to upper tree canopies, for about 85 percent of the diet. Also eats spiders, a few snails, wild fruits, and berries.

REFERENCES: Chapin 1925, Forbush and May 1955, James 1976, Johnsgard 1979, Laurence 1953a.

Black-whiskered Vireo

Vireo altiloquus



RANGE: Breeds in central and southern Florida and on islands in the Caribbean; winters in South America.

STATUS: Common within much of its limited United States range.

HABITAT: Lives mostly in mangroves along the coasts of Florida and the Florida Keys.

SPECIAL HABITAT REQUIREMENTS: Dense mangroves.

NEST: Suspends deep cup nest between twigs (usually in red mangroves but occasionally in other trees or shrubs) as high as 15 feet above the ground or water.

FOOD: Gleans food, primarily spiders, from foliage. Also eats insects, fruits of barberries, and ragweed seeds.

REFERENCES: Bent 1950, Chapin 1925, Sykes in Farrand 1983c, Terres 1980.

Bachman's Warbler

Vermivora bachmanii



RANGE: Formerly bred in northeastern Arkansas, southeastern Missouri, south-central Kentucky, central Alabama, and southeastern South Carolina. May still breed in South Carolina. Winters in Cuba and the Isle of Pines.

STATUS: Rarest songbird in North America; endangered, possibly extinct. Reasons for its decline are not clear.

HABITAT: Inhabits low, moist, deciduous woodlands and swamps of the southern coastal plain, where it probably occurred primarily in sweet bay-swamp tupelo-red maple associations of headwater swamps, sweet gum-willow oak associations of wet flats, and in bottomland hardwoods. Appeared to use forest bottomlands and headwater swamps that were inundated with water for relatively short periods of time.

SPECIAL HABITAT REQUIREMENTS: Mature deciduous swamp forests.

NEST: Locates nest in canebreaks and thickets 2 to 5 feet above the ground in and along the margins of low, wet forested habitats. (Little is known about its nesting habits.)

FOOD: Forages in dense foliage high up in trees for spiders and insects. (Little is known about feeding habits.)

REFERENCES: Griscom and Sprunt 1979, Hooper and Hamel 1977, Mackenzie 1977, Meanley and Mitchell 1958, Sykes in Farrand 1983c.

Blue-winged Warbler

Vermivora pinus



RANGE: Breeds from eastern Nebraska and southeastern Minnesota east to southern Vermont and southern Maine, and south to northwestern Arkansas, northern Alabama, northern Georgia, western South Carolina, and Delaware. Winters in Mexico south to Central America.

STATUS: Uncommon.

HABITAT: Inhabits rank growth near the borders of swamps or streams, woodland edges, brushy overgrown fields and pastures, thickets, and second-growth woods. Prefers old fields with saplings greater than 10 feet tall. Prefers more moist habitats than the golden-winged warbler, a closely related species with which it competes and, in some areas, hybridizes.

SPECIAL HABITAT REQUIREMENTS: Brushy habitats near water.

NEST: Builds nests on the ground, attached to upright stems of weeds or grass clumps. Usually nests in loose aggregations or colonies among bushes, ferns, tangles of vines, or grasses.

FOOD: Gleans insects and spiders from leaves, twigs, and buds among branches near the tops of trees.

REFERENCES: Confer and Knapp 1981, DeGraff et al. 1980, Griscom and Sprunt 1979, Harrison 1975, Johnsgard 1979, Robbins et al. 1983.

Golden-winged Warbler

Vermivora chrysoptera



L 4¼"

RANGE: Breeds from southern Manitoba, central Minnesota, and northern Wisconsin east to southern Vermont and eastern Massachusetts, and south to southeastern Iowa, southern Ohio, and southern Connecticut, and in the Appalachian Mountains south to northern Georgia. Breeding range in the Northeast and Appalachians has been decreasing in recent years, partly as a result of displacement by blue-winged warblers. Winters in Central and South America.

STATUS: Locally common.

HABITAT: Inhabits openings in deciduous forests or forest edges where there is a dense understory of forbs, grasses, or ferns. Also commonly inhabits damp fields heavily vegetated with thick grass, overgrown pastures, dense scrubby thickets, second-growth woods, and brush-bordered lowland areas. Generally occupies higher and drier areas than the blue-winged warbler, although there is a broad overlap in habitats.

SPECIAL HABITAT REQUIREMENTS: Brushy edge habitats or openings in cover with saplings, forbs, and grasses.

NEST: Nests in loose aggregations or colonies on or close to the ground. Usually locates nest within the shade of a forest edge, supported by weed stalks such as goldenrod, or by tufts of grass, or on a substrate of dead leaves.

FOOD: Gleans insects and spiders chickadeelike, from the ground to tree tops.

REFERENCES: Confer and Knapp 1981, DeGraff et al. 1980, Eyer 1963, Griscom and Sprunt 1979, Johnsgard 1979, Parkes in Farrand 1983c, Tate and Tate 1982.

Tennessee Warbler

Vermivora peregrina



L 4¼"

RANGE: Breeds from southeastern Alaska and southern Yukon across Canada to north-central Quebec and southern Labrador, and south to south-central British Columbia, northwestern Montana, northern Minnesota, northeastern New York, and southern Maine. Winters from Mexico to South America.

STATUS: Common.

HABITAT: In northern coniferous and deciduous woodlands, inhabits forest openings with grasses, dense shrubs, and scattered clumps of young trees, open spruce and tamarack or white cedar bogs where sphagnum moss is abundant, brushy hillsides, and occasionally dry pine lands. (Little is known about its breeding biology.)

SPECIAL HABITAT REQUIREMENTS: Brushy, semi-open country.

NEST: Nests singly or sometimes in loose colonies. Conceals nest on moist ground, typically in sphagnum-covered hummocks or among grasses, protected by bog plants overhead, or less frequently, on dry hillsides under the cover of shrubs or saplings.

FOOD: Forages on terminal twigs, gleaning while hopping from branch to branch, eating almost entirely insects. Also eats some spiders and fruits.

REFERENCES: Bent 1953a, DeGraff et al. 1980, Griscom and Sprunt 1979, Johnsgard 1979.

Orange-crowned Warbler

Vermivora celata



L 4¼"

RANGE: Breeds from western and central Alaska and central Yukon across Canada to northern Ontario, central Quebec, and southern Labrador south to southwestern and central California, central Utah, southern New Mexico, and extreme western Texas, and east of the Rockies, to southern Saskatchewan, central Ontario, and south-central Quebec. Winters from coastal and southern California, central Arizona, Texas, the southern portion of the Gulf States, and South Carolina south to Central America.

STATUS: Common in the West; rare in the East.

HABITAT: Occurs in a variety of woodland and brushy habitats, especially sites with considerable shrub cover. Prefers chaparral, brushy open woods, woodland edges of low deciduous growth, burns, overgrown pastures, riparian thickets, and the edges of clearings. In Oregon, found in the mountains up to 6,000 feet, inhabiting dense mixed groves of aspen, alder, willow, and pine in meadows of subalpine parks.

SPECIAL HABITAT REQUIREMENTS: Dense shrubs for nesting.

NEST: Conceals nest on the ground in a bramble tangle, hummock, at the base of a bush or stump, or occasionally up to 3 feet high in low, dense bushes.

FOOD: Gleans insects from foliage in shrubs and small trees at heights ranging from 5 to 30 feet. Also eats some spiders, leaf galls, seeds, and fruits.

REFERENCES: Bent 1953a, Griscom and Sprunt 1979, Harrison 1979, Verner and Boss 1980.

Nashville Warbler

Vermivora ruficapilla



L 4"

RANGE: Breeds from southern interior British Columbia and northwestern Montana south to northwestern and south-central California and extreme west-central Nevada; and from central Saskatchewan to southern Quebec, Nova Scotia, and New Brunswick, south to southern Manitoba, southern Wisconsin, southern Michigan, northern New Jersey, and Rhode Island. Winters from southern Texas south to Mexico and Central America, rarely in California and southern Florida.

STATUS: Common.

HABITAT: Prefers brushy sphagnum bogs and open second-growth woodlands. Also occurs in regenerating areas that have been burned or cut, overgrown pastures and fields, woodland edges, and in swales, slashings, and undergrowth of mixed forests, especially those with aspen or birch. Also found in woodlands, but generally on poor sites.

SPECIAL HABITAT REQUIREMENTS: Scattered trees interspersed with brush.

NEST: Conceals nest on the ground in a small depression, sometimes in a sphagnum hummock, often with an overhead cover of ferns or other overhanging vegetation.

FOOD: Forages from the ground to the treetops, gleaning food (chiefly insects) from the trunk, leaves, and branches, and hawking flying insects.

REFERENCES: DeGraff et al. 1980, Griscom and Sprunt 1979, Johnsgard 1979, Lawrence 1948, Petersen in Farrand 1983c.

Virginia's Warbler

Vermivora virginiae



RANGE: Breeds from east-central California, central Nevada, southeastern Idaho, and southern Wyoming south to south-central California, central and southeastern Arizona, southern New Mexico, and extreme western Texas. Winters in Mexico.

STATUS: Common.

HABITAT: Inhabits arid montane woodlands from 6,000 to 9,000 feet, preferring scrubby brush interspersed with pinyon-juniper and yellow pine. Frequents dense growths of low scrub oaks, mountain-mahogany, and chokecherry, rocky steep slopes and ravines, chaparral, riparian willow and alder thickets, and open spruce and fir forests near scrubby thickets.

SPECIAL HABITAT REQUIREMENTS: Scrubby vegetation for nesting.

NEST: Builds nest on the ground, embedded among dead leaves or in loose soil, sometimes at the base of a bush, or hidden under a tussock of grass, but usually concealed by overhanging vegetation.

FOOD: Forages on the ground, as well as in foliage, and hawks insects on the wing.

REFERENCES: Bent 1953a, Griscom and Sprunt 1979, Terrill in Farrand 1983c, Van Tyne 1936.

Colima Warbler

Vermivora crissalis



L 4¾"

RANGE: Breeds in the Chisos Mountains in extreme western Texas and northern Mexico. Winters in Mexico.

STATUS: Rare and local.

HABITAT: Inhabits forested canyons and slopes between 6,000 and 7,000 feet, where it frequents thickets of young maples and oaks along dry stream beds, clumps of small oaks along mountain slopes, and mixed woods of maple, oak, Arizona cypress, and yellow pine.

SPECIAL HABITAT REQUIREMENTS: Oak thickets above 6,000 feet.

NEST: Nests on the ground among fallen leaves and vines, which may partly or completely conceal the nest. Locates nest on rocky slopes, or adjacent to dry stream beds among small rocks and leaves where there are clumps of small oaks.

FOOD: Occupies the lower tree branches and forages for caterpillars and other insects in Arizona cypress and neighboring vegetation. (No food studies on this species in the United States.)

REFERENCES: Blake 1949, Griscom and Sprunt 1979, Oberholser 1974b, Van Tyne 1936.

Lucy's Warbler

Vermivora luciae



RANGE: Breeds from southeastern California, southern Nevada, and Utah south to southern Arizona, northern Mexico, and extreme western Texas. Winters in western Mexico.

STATUS: Common.

HABITAT: Found in southwestern deserts, generally wherever there are large mesquites, especially along main watercourses. Also occurs in mountain foothills in streamside cottonwoods and willows.

SPECIAL HABITAT REQUIREMENTS: Cavities for nesting.

NEST: The only cavity-nesting warbler besides the prothonotary, places nest in four types of cavities; natural cavities in trees (usually mesquite), where the entrance is in a sheltered spot; under loose bark; in abandoned woodpecker holes; and in deserted verdin nests. Generally locates nest 5 to 6 feet above the ground, but ranges from 1 to 15 feet. Occasionally nests in holes in banks, in yuccas, willows, sycamores, or elderberries.

FOOD: Forages for insects at middle heights in mesquite, seldom in the treetops or near the ground.

REFERENCES: Bent 1953a, Griscom and Sprunt 1979.

Northern Parula

Parula americana



RANGE: Breeds from southeastern Manitoba and central Ontario east to New Brunswick south to south-central and southern Texas, the Gulf Coast, and Florida, and west to the eastern edge of the Plains States. Winters in Florida and from Mexico to Central America.

STATUS: Common.

HABITAT: Primarily associated with swampy woods, especially in the Southeast, where it inhabits mature coniferous and deciduous woodlands where mosslike lichens or Spanish moss are found. In the North, found in swamps and bogs with abundant bearded lichens; in the South, frequents trees draped with Spanish moss. Occasionally occurs in woodlands without moss or lichens.

SPECIAL HABITAT REQUIREMENTS: Bearded lichen (*Usnea*) or Spanish moss (*Tillandsia*) for nesting material or for nest sites.

NEST: Usually suspends nest near the tip of a tree limb that is covered with *Usnea* or *Tillandsia* at heights averaging 10 feet, but ranging from 6 to 100 feet above the ground. Conceals nest with moss or lichen, and constructs it of these materials as well. In areas where they are not available, uses other materials.

FOOD: Forages in a chickadeelike fashion, gleaning insects and spiders from twigs and foliage.

REFERENCES: Bent 1953a, DeGraff et al. 1980, Graber and Graber 1951, Griscom and Sprunt 1979, Johnsgard 1979.

Tropical Parula

Parula pitiayumi



RANGE: Resident from southern Texas in the lower Rio Grande Valley north to near Kingsville, Texas and south locally through Central America into South America. Widespread but local in tropics; largely withdraws in winter from northern limits of range.

STATUS: Scarce; once common, the population in southern Texas has declined, probably because of loss of preferred habitat, pesticide pollution, and the greatly expanded population of bronzed cowbirds.

HABITAT: Found in dense or open woodlands; inhabits undergrowth, brush and trees along the edges of rivers, low dry woodlands, and semiarid cultivated valleys with scattered trees. Breeds from near sea level to 200 feet in elevation in southern Texas, preferring habitats with trees whose branches are draped with Spanish moss.

SPECIAL HABITAT REQUIREMENTS: Air plants (epiphytes) such as Spanish moss for nesting.

NEST: Builds nest 8 to 10 feet above the ground in a hollow formed by a mass of Spanish moss or other air plants that hang in trees or bushes. Nests on relatively level land along rivers and streams, in tall brush or timber.

FOOD: Mostly eats insects. (Little is known about the diet in the United States.)

REFERENCES: Bent 1953a, Griscom and Sprunt 1979, Kaufman in Farrand 1983c, Oberholser 1974b.

Yellow Warbler

Dendroica petechia



RANGE: Breeds from northwestern and north-central Alaska and northern Yukon to northern Ontario, central Quebec, and southern Labrador south to Mexico, central and northeastern Texas, northern Arkansas, central Georgia, and central South Carolina. Winters from southern California, southwestern Arizona, Mexico, and southern Florida south to South America. Also resident in southern Florida.

STATUS: Common; significant population declines in Idaho and the Dakotas, and numbers are declining in many other areas.

HABITAT: Prefers moist habitats such as willow- and alder-lined streams and ponds, brushy bogs, and the edges of marshes, swamps, or creeks. Also occurs in dry sites such as hedgerows, roadside thickets, orchards, farmlands, forest edges, and suburban yards and gardens. Generally occurs wherever patches of trees or shrubs grow, but avoids heavy forests. In the Florida Keys, only inhabits coastal mangroves.

SPECIAL HABITAT REQUIREMENTS: Small scattered trees or dense shrubbery.

NEST: Usually builds nest in an upright fork or crotch of a tree or bush, typically 3 to 8 feet, occasionally up to 40 feet, above the ground. May nest colonially in ideal habitats. Frequently victimized by cowbirds; builds up the nest lining to cover the cowbird eggs.

FOOD: Forages for insects and spiders on the limbs of shrubs and trees by gleaning and hawking.

REFERENCES: Bent 1953a, Biggstone 1913, DeGraff et al. 1980, Griscom and Sprunt 1979, Johnsgard 1979, Schrantz 1943, Tate and Tate 1982, Vickery in Farrand 1983c.

Chestnut-sided Warbler

Dendroica pensylvanica



RANGE: Breeds from east-central Alberta and central Saskatchewan to southern Quebec and New Brunswick south to eastern Colorado, Iowa, central Ohio, and Massachusetts; in the Appalachians south to north-central Georgia and northwestern South Carolina. Winters from Mexico to Panama, casually to South America.

STATUS: Common.

HABITAT: Inhabits rather open and dry areas having some woody vegetation in the form of shrubs and small trees, preferring the brushy regrowth of clear-cut forests and abandoned pastures and fields. Also frequents second-growth woodland edges and clearings, low shrubbery, briar thickets, brushy hillsides and brooksides, and roadside thickets.

SPECIAL HABITAT REQUIREMENTS: Early second-growth moist woodlands with dense vegetation about 3 feet above the ground to provide nest sites and foraging areas.

NEST: Conceals nest from 1 to 4 feet above the ground in briar thickets, bushes, saplings, or vines, such as spirea, raspberry, red-osier dogwood, azalea, laurel, gooseberry, meadow-rue, and hazel.

FOOD: Consumes insects and spiders gleaned from the foliage of shrubs and other low plants, or caught by flycatching. Occasionally eats a few seeds and berries.

REFERENCES: Cripps 1966, Griscom and Sprunt 1979, Lawrence 1948, Tate 1970, Terres 1980, Vickery in Farrand 1983c.

Magnolia Warbler

Dendroica magnolia



RANGE: Breeds from northeastern British Columbia, west-central and southern Mackenzie east to north-central Manitoba and south-central and eastern Quebec, and south to south-central British Columbia, central Saskatchewan, northeastern Minnesota, central Michigan, western Virginia, northwestern New Jersey, and Connecticut. Winters from Mexico to Panama.

STATUS: Common.

HABITAT: Inhabits open coniferous or mixed coniferous-deciduous woodlands, preferring spruce and fir forests with low trees, and coniferous bogs. Also inhabits dense thickets of spruce and fir, old clearings with small coniferous saplings, second-growth following logging, woodland edges, and coniferous thickets along roadsides.

SPECIAL HABITAT REQUIREMENTS: Young conifer stands for nesting.

NEST: Conceals nest in a small conifer, in foliage near the tip of a horizontal branch, generally 1 to 8 feet, but typically less than 5 feet, above the ground. Prefers spruce, fir, and hemlock for nesting, but may use hardwoods.

FOOD: Tends to forage near the center of a tree for insects, rather than at the outer edges; almost entirely insectivorous.

REFERENCES: Bent 1953a, DeGraff et al. 1980, Griscom and Sprunt 1979, Johnsgard 1979, Petersen in Farrand 1983c.

Cape May Warbler

Dendroica tigrina



RANGE: Breeds from southwestern and south-central Mackenzie and northeastern British Columbia east to central Ontario, southern Quebec and New Brunswick south to central Alberta, southeastern Manitoba, northern Wisconsin, southern Ontario, northeastern New York, and east-central Maine. Winters in central and southern Florida and the West Indies.

STATUS: Uncommon.

HABITAT: Inhabits fairly open coniferous forests, especially those with a high percentage of mature spruce. Also frequents dense spruce forests with a scattering of tall spires extending above the canopy level, the edges of coniferous forests, especially if birches or hemlocks are present, and in more open land among small trees. Will occasionally proliferate in areas heavily infested with spruce budworms.

SPECIAL HABITAT REQUIREMENTS: Tall conifer trees, especially spruce, for nesting.

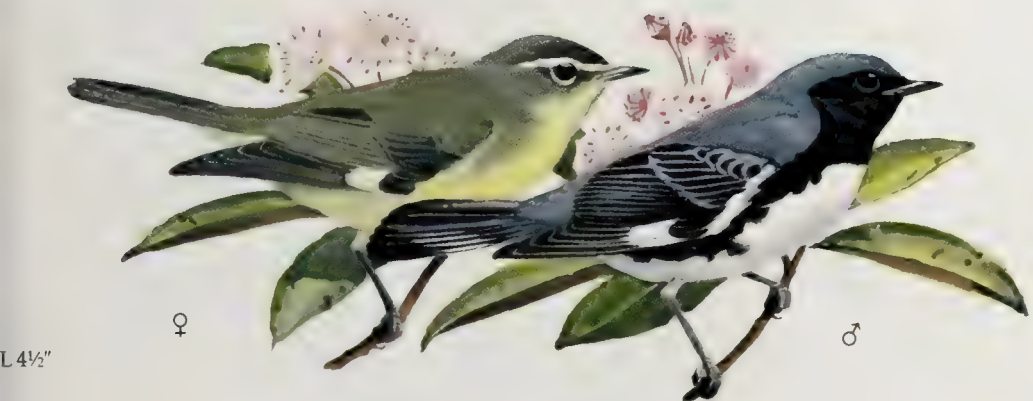
NEST: Builds nest invariably in the uppermost clump of thick foliage near the top of tall conifers, generally invisible from below. (Little is known about the nesting biology of this species, mainly because it tends to nest so high in conifers, and females tend to land near the tree base and move up through the tree rather than fly to the nest.)

FOOD: Consumes insects caught by flycatching or gleaning the tips of dense branches and new buds of conifers near the tops of trees. Also eats spiders and occasionally vineyard grapes.

REFERENCES: Bent 1953a, DeGraff et al. 1980, Griscom and Sprunt 1979, Johnsgard 1979, Petersen in Farrand 1983c.

Black-throated Blue Warbler

Dendroica caerulescens



RANGE: Breeds from western and central Ontario to New Brunswick south to northeastern Minnesota, central Michigan, northeastern Pennsylvania, and southern New England, and in the Appalachians to northeastern Georgia and northwestern South Carolina. Winters primarily from southern Florida to the West Indies, casually in Central and South America.

STATUS: Common.

HABITAT: Prefers northern hardwood forests with an ample undergrowth of saplings and evergreen or deciduous shrubs. Also inhabits mature coniferous-deciduous forests, especially those with an undergrowth of creeping yew, laurel, hazel, maple, or brushy saplings. In the southern Appalachians, often inhabits dense mountain-laurel thickets.

SPECIAL HABITAT REQUIREMENTS: Woodlands with shrubby undergrowth.

NEST: Constructs well-concealed nest near the ground, generally not higher than 3 feet above ground, in fallen tree tops, small trees, or shrubs. Partial to nesting in rhododendron, laurel, hemlock, small spruce, fir, and maple.

FOOD: Forages in the shrub, subcanopy, and lower canopy layers of forests, gleaned insects from foliage and branches. Mostly consumes insects but occasionally eats seeds and berries.

REFERENCES: Bent 1953a, DeGraff et al. 1980, Griscom and Sprunt 1979, Harding 1931, Johnsgard 1979, Petersen in Farrand 1983c.

Yellow-rumped Warbler

Dendroica coronata

L 4¾"

Audubon's

Myrtle

RANGE: The northern and eastern (Myrtle) race breeds from western Alaska and central Mackenzie to north-central Labrador south to northern British Columbia, southeastern Saskatchewan, central Michigan, and Massachusetts, and in the Appalachians to eastern West Virginia. The western (Audubon's) race breeds from central British Columbia and southwestern Saskatchewan south to southern California across to western Texas. The Myrtle race winters from southwestern British Columbia through the Pacific States, southern Arizona, and Colorado, and from Kansas east across the central United States to New England, and south to Panama. The Audubon's race winters from southwestern British Columbia and Idaho south to Central America.

STATUS: Common.

HABITAT: Generally inhabits coniferous forests throughout its range, but also found in aspen forests in the Rocky Mountains. In the West, prefers timbered sites with a low percent canopy cover, and forest edges such as those around meadows or lakes. In the East, prefers spruce-fir woodlands, but also frequents young coniferous growth near the edges of woods, mixed woods, and evergreen plantations.

SPECIAL HABITAT REQUIREMENTS: Coniferous trees for nesting.

NEST: Builds nest well out on a horizontal branch in a conifer tree, screened from above by clumps of needles. Typically locates nest 15 to 20 feet above the ground, but sometimes 4 to 50 feet.

FOOD: Eats insects gleaned from foliage and caught by hawking. Also searches for food on the ground. In winter, largely subsists on berries.

REFERENCES: Beal and McAtee 1912, Bent 1953a, DeGraff et al. 1980, Griscom and Sprunt 1979, Johnsgard 1979, Kaufman in Farrand 1983c, Verner and Boss 1980.

Black-throated Gray Warbler

Dendroica nigrescens



RANGE: Breeds from southwestern British Columbia and western Washington to northern Utah and southern Wyoming south, primarily in mountains, to northern Baja California, central and southeastern Arizona, extreme western Texas, and Mexico. Winters from coastal southern California and southern Arizona south to Mexico.

STATUS: Common.

HABITAT: In the northern portion of its range, inhabits conifer forests that are open and interspersed with shrubs or forest edges. Farther south, seems to prefer shrubby stands of oaks, pinyon, juniper, and manzanita. Throughout its range, prefers and is perhaps limited to dry slopes.

NEST: In Washington, seems to nest exclusively in fir trees, placing nest on horizontal branches 7 to 50 feet above the ground. In habitats further south, builds nests in shrubs such as manzanita, oak, ceanothus, or large white oaks and sycamores.

FOOD: Forages among the leaves of shrubs for insects. (Detailed food habits have not been reported.)

REFERENCES: Bent 1953a, Griscom and Sprunt 1979, Phillips et al. 1964.

Townsend's Warbler

Dendroica townsendi



RANGE: Breeds from east-central Alaska, southern Yukon, and coastal British Columbia, as well as parts of Alberta and Saskatchewan, south along the Pacific Coast into northwestern Washington, and inland to central and southeastern Washington, central and northeastern Oregon, northern Idaho, northwestern and south-central Montana, and northwestern Wyoming. In general, breeding distribution follows that of conifers and mixed coniferous-deciduous forests. Winters in the coastal region of Oregon and California south through the highlands of Mexico and Central America to Costa Rica.

STATUS: Common in coniferous forests of the Pacific Northwest.

HABITAT: During breeding season, primarily inhabits tall coniferous forests of the Pacific Northwest, most commonly the more mountainous regions, usually near the crowns of tall trees. During migration and winter, moves into humid forests as well as pine-oak associations, open woodlands, and second-growth scrub forests.

SPECIAL HABITAT REQUIREMENTS: Tall, coniferous forests of the north Pacific Coast.

NEST: Nests in conifers, particularly firs, generally on the limb of the tree and not in the fork or crotch. Constructs nests of bark and slender twigs woven together, usually places them near the crowns of trees. In shorter trees, places nests as close as 10 or 12 feet to the ground.

FOOD: Consumes insects found on the needles of conifers as primary diet during spring and summer. (Winter food habits are not well documented.)

REFERENCES: Bent 1953a, Griscom and Sprunt 1979.

Hermit Warbler

Dendroica occidentalis

L 4¼"



RANGE: Breeds in coniferous forests from southern British Columbia south through the coastal ranges and Sierra Nevadas to southern California. Winters in Mexico and Central America. In general, distribution coincides with tall coniferous trees.

STATUS: Uncommon and local in summer habitats.

HABITAT: Uses very tall conifers, including Douglas-fir and cedar. Prefers scattered groups of tall trees (sometimes 200 or more feet tall) that tower above the rest of the forest. Generally found in the upper canopies of tall trees, and though very active, are often difficult to identify.

SPECIAL HABITAT REQUIREMENTS: Tall coniferous trees.

NEST: Builds a well-concealed nest, generally supported by needles on the scraggly limbs of conifers, often up to 40 or 50 feet above the ground. Generally forage on the upper portions of trees, while nests are built in the mid-canopy of some of the tall trees.

FOOD: Feeds on a variety of insects found in the upper level of coniferous trees, gleaning them from needles and twigs, or hawking flying insects.

REFERENCES: Bent 1953a, Griscom and Sprunt 1979.

Black-throated Green Warbler

Dendroica virens



RANGE: Breeds from east-central British Columbia and northern Alberta to central Ontario and Newfoundland south to central Alberta, southern Manitoba, central Minnesota, Pennsylvania, and northern New Jersey, and south in the mountains to northern Alabama and Georgia. Winters from southern Texas and southern Florida south to Central America and the West Indies.

STATUS: Common.

HABITAT: Inhabits open mixed woodlands (especially northern hardwood-hemlock stands), northern coniferous forests with large trees, and larch bogs. Less often, inhabits second-growth hardwoods and pastures with cedars. It occurs rather commonly in pine barrens in Maine and jack pines in Michigan.

SPECIAL HABITAT REQUIREMENTS: Some coniferous cover.

NEST: Builds a compact, deep cup nest, usually placed on a branch or in a fork of a conifer tree, 3 to 80 feet above the ground; occasionally uses a deciduous tree.

FOOD: Largely consumes insects gleaned from leaves and branches, and occasionally hawks flying insects.

REFERENCES: Griscom and Sprunt 1979, Harrison 1975, Pitelka 1940, Terres 1982.

Golden-cheeked Warbler

Dendroica chrysoparia



L 4 1/4"

RANGE: Breeds from central Texas south to the Edward's Plateau region into Medina and Bexar Counties and west to Real and Kerr Counties. Winters in the highlands of Central America. Occasionally visits the Farallon Islands of California and isolated areas of Florida.

STATUS: Uncommon and very local.

HABIAT; Prefers small stands of mountain-cedar on rough woody hillsides in canyons or on ridges that separate headwaters of streams, and also inhabits mountain oak, black oak, and live oak thickets on higher grounds as well as oak thickets on the lower flats along the foothills. Populations have been eliminated by removal of "cedar brakes." Mature cedar brakes ranging from several hundred acres to a thousand or more are necessary to insure habitat for this specie.

SPECIAL HABITAT REQUIREMENTS: Mountain-cedar in canyons or draws within 1-1/2 miles of water.

NEST: Builds nests of cedar bark interspersed with webs, often from spiders. Fastens nests to limbs in the mid-canopy level of mountain-cedars and are difficult to locate because they resemble the bark of the tree. Often parasitized by cowbirds.

FOOD: Eats a variety of insects and spiders.

REFERENCES: Griscom and Sprunt 1979, Oberholser 1974b, Pulich 1976.

Blackburnian Warbler

Dendroica fusca



RANGE: Breeds from central Alberta east to southern Quebec and Nova Scotia south to southern Manitoba, northeastern Ohio, Pennsylvania, and southeastern New York, and in the Appalachians to South Carolina and northern Georgia. Winters in Central and South America.

STATUS: Common.

HABITAT: Throughout most of its range, favors mature conifer forests with a few deciduous trees, preferring the upper canopy of tall conifers. Also inhabits climax stands of conifers with sparse understory and with deciduous trees and shrubs around the edges. In the Appalachians, inhabits oak-hickory forests along ridges.

SPECIAL HABITAT REQUIREMENTS: Tall coniferous forests; oaks in the Appalachians.

NEST: Builds a deeply cupped nest saddled to a horizontal branch of a large tree. Nests in conifers throughout its range but also uses deciduous trees in the South. Usually locates nest high (up to 80 feet) above the ground and well out from the tree trunk.

FOOD: Consumes mostly insects gleaned from branches and leaves, but also flying insects caught in the air. Eats some berries when insects are scarce.

REFERENCES: Bull and Farrand 1977, Griscom and Sprunt 1979, Lawrence 1953b, Terres 1982.

Yellow-throated Warbler

Dendroica dominica



L 4½"

RANGE: Breeds from southeastern Kansas, central Ohio, and central New Jersey south to south-central and eastern Texas, the Gulf Coast, central Florida, and the northern Bahama Islands. Wanders north to the Great Lakes and the Maritime Provinces. Winters from southeastern Texas, the Gulf Coast, and South Carolina south to Costa Rica.

STATUS: Common in southeastern United States.

HABITAT: Generally inhabits large trees along river banks, swamps, and bottomlands, as well as open stands of pines, live oaks, and mixed forests. In the South, prefers forests with abundant Spanish moss. Tends to utilize the upper canopy level of the forests.

NEST: In coastal areas, nearly always builds nest in clumps of Spanish moss. In areas with no Spanish moss, saddles nest on a horizontal branch. Locates nests 10 to 100 feet above the ground, generally far out from the tree trunk.

FOOD: Is a skillful "fly catcher," but gleans much of its food from leaves and branches; eats nearly all insects.

REFERENCES: Bull and Farrand 1977, Griscom and Sprunt 1979, Harrison 1975, Johnsgard 1979, Sykes in Farrand 1983, Terres 1982.

Grace's Warbler

Dendroica graciae



RANGE: Breeds from southern Nevada, southern Utah, southwestern Colorado, northern New Mexico, and western Texas south through the mountains of western Mexico to Nicaragua. Winters in northern Mexico; resident from central Mexico southward.

STATUS: Locally common in pine-oak forests above 7,000 feet.

HABITAT: Typically inhabits pine forests, usually in the upper portions of yellow pines. Sometimes inhabits hemlock and fir woodlands, and occasionally oak thickets; generally from 6,000 to 9,000 feet.

SPECIAL HABITAT REQUIREMENTS: Pine forests approximately 7,000 feet in elevation.

NEST: Locates nest on limbs of pine trees up to 60 feet above the ground, sometimes in the middle of bunches of pine needles. Builds a very compact nest composed of a variety of grass fibers, hair, vegetable material, and insect webbing, often hidden from view.

FOOD: Commonly gleans food (almost entirely insects) from leaves and branches of pines, as well as hemlocks and spruces. Most commonly forages in the very upper canopies of the tree, but sometimes catches flying insects on the wing.

REFERENCES: Griscom and Sprunt 1979.

Pine Warbler

Dendroica pinus



RANGE: Breeds from southern Manitoba, western Ontario, southwestern Quebec, and central Maine south to eastern Texas, the Gulf Coast, southern Florida, and the Bahamas. Rare or absent in the upper Mississippi and Ohio River Valleys. Winters in the southeastern United States south to southern Texas, the Gulf Coast, and southern Florida into Mexico.

STATUS: Common to rare and local.

HABITAT: Inhabits open pine forests and pine barrens, especially jack pine in Minnesota and upland southern pines. Generally avoids tall, moist, and dense coniferous forests.

SPECIAL HABITAT REQUIREMENTS: Open pine forests.

NEST: Builds nests saddled on horizontal limbs of conifers 8 to 80 (usually 30 to 50) feet above the ground, usually far out from the tree trunk and well concealed in foliage.

FOOD: Gleans its food from tree trunks, larger branches, and leaves. In the summer, mostly eats insects and some spiders. In winter, also eats pine seeds, wild fruits and berries, and grass and weed seeds.

REFERENCES: Bull and Farrand 1977, Griscom and Sprunt 1979, Harrison 1975.

Kirtland's Warbler

Dendroica kirtlandii



L 4¾"

RANGE: Breeds only in extensive tracts of small jack pines in a few counties of northern lower Michigan. Occasionally strays to similar habitats in Wisconsin, southern Ontario, and southern Quebec if not breeding. Winters throughout the Bahamas.

STATUS: Endangered. Approximately 1,000 birds in existence.

HABITAT: Breeds in very specific habitats : extensive stands (80 + acres) of young jack pine that are 6 to 20 feet tall and have living pine branches near the ground. Usually moves into burned-over jack pine forests 6 to 13 years after fire and inhabits these young forests for 10 to 12 years.

SPECIAL HABITAT REQUIREMENTS: Dense stands of young jack pine.

NEST: Tends to nest in loose colonies. Conceals nest under low vegetation (particularly bluestem grass and blueberry) near the base of a small jack pine on flat, dry, porous soil, usually depressed below ground level; about half of nests are parasitized by brown-headed cowbirds.

FOOD: Gleans food (mostly insects) from the ground and pine needles.

REFERENCES: Griscom and Sprunt 1979, Mackenzie 1977, Mayfield 1960.

Prairie Warbler

Dendroica discolor



RANGE: Breeds from eastern Nebraska, central Missouri, northern Illinois, central Wisconsin, northern Michigan, southern Ontario, southeastern New York and New Hampshire south to eastern Texas, the Gulf Coast and southern Florida. Winters from central Florida south to the West Indies and Central America.

STATUS: Common.

HABITAT: Generally inhabits open brushy lands, often in mixed pine and scrub oak woodlands. Also inhabits southern pine forests, sand dunes, mangroves, and jack pine plains but tends to avoid dense forests. (Suitable habitats have increased on abandoned farms, unmowed orchards, strip mine lands, Christmas tree farms, and burned and grazed woodlands.)

SPECIAL HABITAT REQUIREMENTS: Low trees and shrubs; tends to favor areas with some conifers.

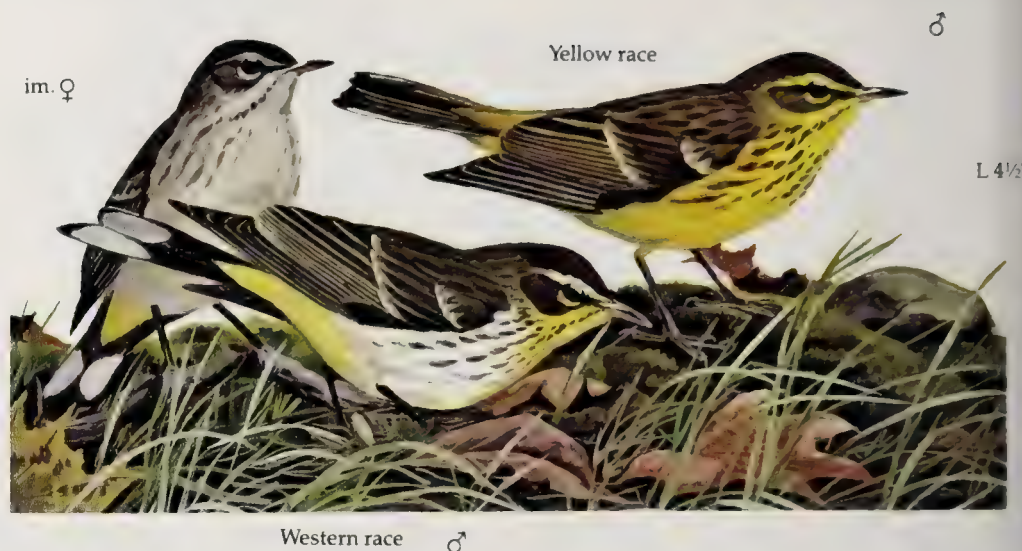
NEST: Sometimes nests in loose colonies. Attaches well-concealed cup nest to stems and branches of a variety of shrubs and trees, usually 2 to 3 feet above the ground.

FOOD: Gleans food from tree leaves, branches, and the ground, but also catches flying insects in the air. Eats mostly insects, but also eats some snails and worms.

REFERENCES: Griscom and Sprunt 1979, Nolan 1978.

Palm Warbler

Dendroica palmarum



RANGE: Breeds from southern Mackenzie and northern Alberta to central Quebec and southern Newfoundland south to northeastern British Columbia, central Alberta, northern Minnesota, southern Quebec, Maine, and Nova Scotia. Winters mostly from north-central Texas to North Carolina south to southern Texas, the Gulf Coast, southern Florida, and islands in the Caribbean.

STATUS: Fairly common.

HABITAT: Inhabits boggy areas dominated by tamarack, black spruce, and white cedar, and dry, open forests of spruce or jack pine.

NEST: Sometimes nests in loose colonies. Usually builds nest on the ground, nearly buried in sphagnum mosses, but may nest in the low branches of conifer saplings.

FOOD: Forages on the ground, gleans food from twigs and conifer cones, and also catches flying insects. Mainly eats insects, but also some vegetable matter, especially barberries during winter.

REFERENCES: Bent 1953b, Griscom and Sprunt 1979.

Bay-breasted Warbler

Dendroica castanea



RANGE: Breeds from southwestern Mackenzie to north-central Saskatchewan and Newfoundland south to northeastern British Columbia, southern Manitoba, and northeastern Minnesota to southern Maine. Winters in northern South America.

STATUS: Fairly common.

HABITAT: Inhabits northern coniferous forests or mixed forests, favoring young spruce and fir. Also found in woodlands bordering streams, along fence rows and highways, and in mixed woods around ponds and lakes. During migration, uses all types of woodlands but prefers conifers.

SPECIAL HABITAT REQUIREMENTS: Early stages of second-growth conifer forests.

NEST: Usually saddles nest on a horizontal branch of a conifer, 4 to 40 feet above the ground, well out from the tree trunk.

FOOD: Forages among the middle and upper branches of small conifers to glean food from needles and flowers. Eats mostly insects; occasionally eats berries such as Virginia creepers and mulberries in the fall.

REFERENCES: Griscom and Sprunt 1979, Harrison 1975, Mendall 1937.

Blackpoll Warbler

Dendroica striata

L 4½"



RANGE: Breeds from western and north-central Alaska throughout most of central Canada around the lower part of Hudson Bay to the Atlantic Coast, coincidental with boreal forests. Migrates south across the eastern United States and winters in South America.

STATUS: Common throughout the north-central boreal forests.

HABITAT: Inhabits northern coniferous forests, favoring stunted, young or medium-sized conifers, especially the upper canopy. Migrates primarily at night and is often attracted to bright lights. (Probably one of the most common species seen in migration, when large numbers are found in gardens and parks.)

SPECIAL HABITAT REQUIREMENTS: Northern coniferous forests. Requires conifers for nesting and prefers spruce.

NEST: Builds a generally bulky nest of a variety of twigs, bark, and sometimes moss and grass, lined usually with plant fiber, grass, hair, and rootlets. Often locates nest 2 to 7 feet above the ground, usually near the trunk of a tree, supported by horizontal branches, and quite well concealed.

FOOD: Primarily eats insects, gleaning adults and larvae from leaves and twigs, and catching insects in flight. Probes into galls and other protusions of trees and will also eat seeds and berries in the fall.

REFERENCES: Griscom and Sprunt 1979.

Cerulean Warbler

Dendroica cerulea



L 4"

RANGE: Breeds from southeastern Minnesota, southern Wisconsin, southern Michigan, Ontario, New York, and western New England south to northeastern Texas, southeastern Louisiana, Mississippi, Alabama, and central North Carolina. Winters in South America.

STATUS: Locally common.

HABITAT: Favors moist deciduous swamp and bottomland forests and shady, mature upland woods. Prefers rather open forests with tall trees and little undergrowth.

SPECIAL HABITAT REQUIREMENTS: Tall deciduous trees.

NEST: Usually builds nest 15 to 90 feet above ground in tall trees, well away from the trunk, on horizontal branches that are free from vegetation below. In some parts of the range, favors elm for nesting, but will nest in oaks, maples, basswood, and yellow-poplar.

FOOD: Eats mostly insects gleaned from leaves or caught in the air.

REFERENCES: Armistead in Farrand 1983c, Bent 1953a, DeGraff et al. 1980, Griscom and Sprunt 1979, Johnsgard 1979.

Black-and-white Warbler

Mniotilta varia



L 4½"

RANGE: Breeds from west-central Mackenzie, northern Alberta, and central Saskatchewan to southern Quebec and Newfoundland; south to eastern Montana, central Texas, Louisiana, Alabama, Georgia, and North Carolina. Winters from southern Texas and Florida through Mexico to South America.

STATUS: Common.

HABITAT: Generally associated with semiopen upland stands of deciduous or mixed forests; usually not abundant in coniferous forests. Found in mature and second-growth forests, especially those composed of immature or scrubby trees.

NEST: Builds nest in a slight depression in the ground, usually at the base of a tree or stump, beside a log, or sometimes in the roots of a fallen tree.

FOOD: Mainly eats insects, but it also gleans many spiders and daddy longlegs from tree trunks and larger tree limbs.

REFERENCES: Bent 1953a, Forbush and May 1955, Griscom and Sprunt 1979, Smith 1934.

American Redstart

Setophaga ruticilla



RANGE: Breeds from southeastern Alaska, east to Labrador and Newfoundland south to Utah, southeastern Oklahoma, and east Texas to South Carolina. Absent as a breeding bird through most of the Great Plains region. Winters from Baja California, southern Texas, and central Florida south to Brazil.

STATUS: Abundant.

HABITAT: Prefers open deciduous woodlands with a good understory of shrubs and young trees but is very adaptable. Frequently nests in mixed coniferous-deciduous forests, shade trees and shrubbery around farms, orchards, and willow and alder thickets bordering ponds and streams.

NEST: Normally builds its nest 10 to 20 feet above the ground in a crotch or on a horizontal limb of a second-growth deciduous tree. Frequently parasitized by brown-headed cowbirds when nesting outside of woodlands.

FOOD: Chiefly eats insects caught in the air or gleaned from leaves and branches. Also eats some spiders, daddy longlegs, and fruits.

REFERENCES: Baker 1944, Griscom and Sprunt 1979, Vickery in Farrand 1983c.

Prothonotary Warbler

Protonotaria citrea



RANGE: Breeds from east-central and southeastern Minnesota, south-central Wisconsin, southern Michigan, southern Ontario, central New York and northern New Jersey south to south-central and eastern Texas, the Gulf Coast and central Florida, and west to eastern Oklahoma, eastern Kansas, and central Oklahoma. Winters rarely in Florida and extreme south; otherwise, migrates to eastern Central America and South America.

STATUS: Uncommon.

HABITAT: Generally associated with moist, bottomland, or swampy deciduous woods, including woods that are frequently flooded and willow-lined streamsides.

SPECIAL HABITAT REQUIREMENTS: Moist woodlands with cavities for nesting.

NEST: Nests in natural cavities and old cavities of woodpeckers (especially downy woodpeckers) and chickadees in stumps or snags that are standing in or near water. Will occasionally nest in nest boxes. Usually places nest low, about 5 feet above the ground.

FOOD: Primarily eats insects gleaned from tree trunks and branches, shrubs, and fallen logs.

REFERENCES: Bent 1953a, Forbush and May 1955, Griscom and Sprunt 1979, Pearson 1936, Walkinshaw 1953.

Worm-eating Warbler

elmitheros vermivorus



L 4½"

RANGE: Breeds from southeastern Nebraska, southeastern Iowa to southern and east-central Ohio and Massachusetts, south to southeastern Oklahoma and northeastern Texas to northern Florida. Winters in the West Indies, Mexico, and Central America.

STATUS: Locally common to rare.

HABITAT: Inhabits wooded hillsides and ravines with medium-sized stands of deciduous trees and undergrowth, often near streams or swampy bogs rimmed by shrubs and vines.

SPECIAL HABITAT REQUIREMENTS: Dense undergrowth.

NEST: Builds nest on the ground at the base of a tree or sapling, usually well concealed under dead leaves. Generally locates nest on a hillside or bank of a ravine, but sometimes in a bank cavity or under shrubbery.

FOOD: Gleans its food from the ground; mostly eats insects but some spiders and a few worms.

REFERENCES: DeGraff et al. 1980, Griscom and Sprunt 1979.

Swainson's Warbler

Limnothlypis swainsonii



L 5"

RANGE: Breeds locally from northeastern Oklahoma, southern Missouri, southern Illinois, southwestern Indiana, southwestern and eastern Kentucky, southern Ohio, western West Virginia, western and southern Virginia, and southern Delaware south to east-central Texas, the Gulf Coast, and northern Florida. Winters on the Caribbean islands and in southeast Mexico.

STATUS: Uncommon.

HABITAT: Generally inhabits rich, damp woodlands with deep shade and dense undergrowth, including wooded swamps and canebrakes of lowlands and, locally, rhododendron thickets of the mountains.

SPECIAL HABITAT REQUIREMENTS: Dense underbrush.

NEST: Builds a large bulky nest, usually 2 to 6 feet above the ground. In coastal lowlands, commonly nests in cane or palmetto; in highlands, nests in shrubs, small trees, vines, briars, rhododendron, or laurel. Sometimes parasitized by cowbirds.

FOOD: Consumes primarily insects and spiders found in leaves on the ground, but occasionally searches for food in low shrubs.

REFERENCES: Harrison 1975, Meanley 1966, 1971.

Ovenbird

Seiurus aurocapillus

L 5"



RANGE: Breeds from northeastern British Columbia, southern Mackenzie, northern Alberta, across southern Canada to Newfoundland south to eastern Colorado, eastern Oklahoma, northern Arkansas, and the mid-Atlantic States to northern Georgia. Winters in coastal South Carolina, Florida, the Gulf States, coastal Texas, the West Indies, Mexico, and Central America.

STATUS: Common.

HABITAT: Usually inhabits open, mature, dry, deciduous forests without thick brush and tangles, preferring areas with an abundance of fallen leaves, logs, and rocks. Occasionally inhabits wet or swampy forests; in the North, inhabits jack pine and spruce forests.

NEST: Locates nest in a slight depression in the ground. Uses almost any available vegetation to construct an arched nest resembling a dutch oven, with the entrance hole at or near ground level.

FOOD: Gleans invertebrate food from the surface of the litter on the forest floor, including insects, small snails, slugs, myriapods, earthworms, and spiders.

REFERENCES: DeGraff et al. 1980, Griscom and Sprunt 1979, Hann 1937, Stenger 1958, Vickery in Farrand 1983c.

Northern Waterthrush

Seiurus noveboracensis



RANGE: Breeds from Alaska and southern Mackenzie across Canada to central Labrador and Newfoundland, south to northwestern Washington and east to central Michigan, northeastern Ohio, southeastern West Virginia, Pennsylvania, New York, and Massachusetts. Winters mostly from Mexico to South America and the West Indies.

STATUS: Locally common.

HABITAT: Generally inhabits thickets along edges of swamps, ponds, and wooded streams with numerous fallen trees. Prefers woodlands and shrubs around standing water rather than moving streams.

SPECIAL HABITAT REQUIREMENTS: Cool, shady, wet, brushy areas with open pools.

NEST: Builds nests on the ground among fallen trees, at the base of living trees, in cavities of rotten stumps, and under overhanging banks or cuts.

FOOD: Gleans food from moist soil and litter, consuming aquatic and terrestrial insects, small crustaceans, mollusks, and some minnows and worms.

REFERENCES: Griscom and Sprunt 1979, Johnsgard 1979, Petersen in Farrand 1983c.

Louisiana Waterthrush

Geothlypis trichas



L 5¼"

RANGE: Breeds from eastern Nebraska, central Iowa, and east-central Minnesota to central New York and New England, south to eastern Texas, central Louisiana, central Georgia, and the Carolinas. Winters in the West Indies, Mexico, and northern South America.

STATUS: Uncommon.

HABITAT: Favors bottomland forests with moss-covered logs and rank undergrowth along rapidly moving streams. Also sometimes inhabits shrub-grown bogs or areas near swamp pools or lake edges.

SPECIAL HABITAT REQUIREMENTS: Woodlands with flowing water.

NEST: Typically builds nest on the ground under roots, or in cavities in steep banks along streams. Also nests in cavities of upturned roots of fallen trees over or near water.

FOOD: Searches for food along sandy margins of streams, where it eats aquatic and terrestrial insects, spiders, small mollusks, killifishes, and snails.

REFERENCES: Eaton 1958, Griscom and Sprunt 1979, Petersen in Farrand 1983c.

Kentucky Warbler

Oporornis formosus



RANGE: Breeds from southeastern Nebraska, southwestern Wisconsin, southern Michigan, central Ohio, southern Pennsylvania, and southeastern New York south to eastern Texas, the Gulf Coast, central Georgia, and South Carolina. Casual in southwestern States. Winters from Mexico south to northern South America.

STATUS: Common.

HABITAT: Inhabits shrubby woodland borders and the understory of damp or shady deciduous woods, favoring moist ravines and bottomlands. Often found near water and at low elevations.

NEST: Generally builds nest on the ground among plants at the base of shrubs and trees, or under branches of fallen limbs. Occasionally places nest near the ground in shrubs. Commonly victimized by brown-headed cowbirds.

FOOD: Gleans most food from leaves on the ground, but occasionally catches insects from low leaves and branches. Mostly eats spiders and insects.

REFERENCES: DeGaris 1936, Griscom and Sprunt 1979, Sykes in Farrand 1983c.

Connecticut Warbler

Oporornis agilis



RANGE: Breeds from east-central British Columbia east across Canada to west-central Quebec, and south to southern Manitoba, northern Minnesota, northern Wisconsin, central Michigan, and south-central Ontario. Winters in South America.

STATUS: Uncommon and local.

HABITAT: Generally inhabits cold, damp black spruce and tamarack bogs, and prefers areas with scattered trees and grassy openings. At the extremes of the breeding range, inhabits well-drained ridges or poplar and aspen woods.

NEST: Conceals nest in a mound of moss or beside a clump of dry grass on or near the ground. Usually nests in open forests with widely spaced trees such as aspen and balsam.

FOOD: Mostly eats spiders gleaned from the ground or low branches, but also eats insects, their larvae and eggs.

REFERENCES: Griscom and Sprunt 1979, Walkinshaw and Dyer 1961, Harrison 1975.

Mourning Warbler

Oporornis philadelphia



RANGE: Breeds east of the Rocky Mountains across Canada and the northern United States from northeastern British Columbia to Newfoundland south to North Dakota and central New England through the Appalachian Mountains to Virginia. Winters in Central America and northwestern South America.

STATUS: Locally common to uncommon.

HABITAT: Inhabits shrubby second-growth, dense undergrowth in open woods, shrubby margins of lowland swamps or bogs, and forest clearings or burned areas that have brambles, shrubs, and saplings. May occur in partially open coniferous and deciduous woodlands with herb and shrub understories.

SPECIAL HABITAT REQUIREMENTS: Extensive stands of saplings or dense shrubs.

NEST: Conceals nests in dense herbaceous or shrubby vegetation on or near the ground. Tends to nest in edges along woodland or clearing edges, logging trails, or at the edges of bogs and marshes.

FOOD: Generally gleans beetles, lepidopterans, and spiders from the ground or low shrubs. (Detailed food habits have not been studied.)

REFERENCES: Cox 1960, DeGraff et al. 1980, DeSante in Farrand 1983c, Griscom and Sprunt 1979.

MacGillivray's Warbler

Oporornis tolmiei



RANGE: Breeds from southeastern Alaska, southwestern Yukon, northern British Columbia, southern Alberta, northwestern Saskatchewan, and southwestern South Dakota south, primarily in the mountains, to southern California, central Arizona, and southern New Mexico. Winters from northern Mexico to Panama.

STATUS: Common to uncommon.

HABITAT: Prefers early successional stages of cutover or burned woodlands or low shrubby habitats. Also inhabits low vegetation such as blackberry, salmonberry, cherry, currant, serviceberry, snowberry, poison oak, ninebark, spirea, and riparian willow and alder.

SPECIAL HABITAT REQUIREMENTS: Low vegetation.

NEST: Prefers dense, moist, brushy habitat, or areas with tall weeds or ferns for nesting. Builds nest 2 to 5 feet above the ground, attached to several stalks of plants.

FOOD: Forages close to the ground in dense thickets, where it gleans insects from the vegetation. (No comprehensive food studies have been made.)

REFERENCES: DeSante in Farrand 1983c, Griscom and Sprunt 1979, Terres 1980.

Common Yellowthroat

Geothlypis trichas



RANGE: Breeds from southeastern Alaska to northern Alberta and Newfoundland south to northern Baja California, Mexico, and southern Texas, the Gulf Coast and southern Florida. Winters along the Pacific Coast, from northern California across southern Arizona, central Texas, and southern Arkansas to the Gulf States, and along the Atlantic Coast from New Jersey, Virginia, and Delaware to Florida; also in the Bahamas, West Indies, Mexico, and Central America.

STATUS: Common to abundant.

HABITAT: Typically inhabits areas with a mixture of dense, lush herbaceous vegetation with small woody plants (mainly shrubs and small trees), in damp or wet situations. Occasionally found in dry thickets or dense undergrowth in open woodlands.

SPECIAL HABITAT REQUIREMENTS: Dense growth of low vegetation.

NEST: Builds a bulky cup nest of grass, leaves, and bark, well hidden on the ground in a grass tussock or similar vegetation. Occasionally locates nest in shrubs or a tangle of briars up to 3 feet above the ground.

FOOD: Gleans insects and spiders from leaves of shrubs, grasses, and forbs.

REFERENCES: Griscom and Sprunt 1979, Hofslund 1959, Low and Mansell 1983, Stewart 1953, Terres 1980.

Hooded Warbler

Wilsonia citrina



RANGE: Breeds from southeastern Iowa, northern Illinois, and extreme southern Michigan and Ontario, southern New York, and New England south to eastern Texas, the Gulf of Mexico, and northern Florida. Winters from Mexico to Panama.

STATUS: Common.

HABITAT: Generally inhabits moist, forested regions of mixed hardwoods of beech, maple, hickory, and oak with dense undergrowth. In the Southeast, also inhabits cypress-gum swamplands.

SPECIAL HABITAT REQUIREMENTS: Low, dense, deciduous woody vegetation.

NEST: Builds a cuplike nest, usually in a fork of saplings, shrubs, or in herbaceous vegetation, less than 5 feet above the ground.

FOOD: Primarily eats insects, and some spiders. Is an expert "flycatcher."

REFERENCES: Armistead in Farrand 1983c, Bent 1953b, Griscom and Sprunt 1979, Odum 1931.

Wilson's Warbler

Wilsonia pusilla



RANGE: Breeds from northern Alaska, northern Yukon, northern Ontario, southeastern Labrador, and Newfoundland south to southern California, central Nevada, northern Utah, northern New Mexico, central Ontario, northern New England, and Nova Scotia. Winters from southern California and southern Texas to Panama.

STATUS: Common.

HABITAT: Prefers wet clearings in early stages of regeneration. Also inhabits peat or laurel bogs with scattered young or dwarf spruces and tamaracks, and riparian willow and alder thickets.

SPECIAL HABITAT REQUIREMENTS: Shrubby vegetation.

NEST: Generally nests on the ground, sometimes in loose colonies. Usually builds nest at the base of a small tree or shrub, often well concealed in a grass hummock. Occasionally, places nest above the ground in low, dense tangles of vegetation.

FOOD: Mostly eats insects (about 93 percent of diet) gleaned from the ground and twigs or caught by flycatching. Also eats some spiders and fruit pulp.

REFERENCES: Beal 1907, Bent 1953b, Griscom and Sprunt 1979, Petersen in Farrand 1983c, Stewart 1973.

Canada Warbler

Wilsonia canadensis



RANGE: Breeds from central Alberta east to southern Quebec and Nova Scotia south to southern Manitoba, central Minnesota, central Michigan, and through the Appalachian Mountains to northern Georgia. Winters in South America.

STATUS: Locally common.

HABITAT: Inhabits a variety of vegetative types from lowlands to uplands and coniferous to deciduous. Favors shrubby undergrowth in cool, moist, mature woodlands, streamside thickets, and weedy ravines. In the southern highlands, lives in rhododendron thickets.

NEST: Builds nest on or near the ground on mossy logs or stumps, in cavities in banks, among roots of fallen trees, or in mossy hummocks.

FOOD: Mostly eats insects and spiders caught by flycatching or gleaned from the ground.

REFERENCES: Bent 1953b, Griscom and Sprunt 1979, Krause 1965, Petersen in Farrand 1983.

Red-faced Warbler

Cardellina rubrifrons



L 4½"

RANGE: Breeds from central Arizona and southwestern New Mexico south into Mexico to western Durango. Winters in the highlands of Mexico to El Salvador and western Honduras.

STATUS: Locally common.

HABITAT: Prefers Douglas-fir and Engelmann spruce forests at elevations of 6,500 to 9,000 feet, but also inhabits ponderosa pine, oak, aspen, and riparian stands and seems to favor southern exposures.

NEST: Places nest nearly always on the ground, concealed beneath or beside a sheltering log, rock, sapling, or tuft of grass, usually on a well-drained bank or hillside.

FOOD: Searches for food through the outer branches of conifer trees and flycatches. Primarily eats insects. (Food habits have not been studied.)

REFERENCES: Griscom and Sprunt 1979, Scott and Gottfried 1983.

Painted Redstart

Myioborus pictus



L 4½"

RANGE: Breeds from northwestern and central Arizona, southwestern New Mexico, and western Texas south through the mountains of Central America to Nicaragua; casually in southern California. Winters from northwestern Mexico south through the breeding range.

STATUS: Common.

HABITAT: Mainly inhabits timbered desert mountain canyons, gulches, and rugged slopes in coniferous and deciduous woodlands, generally near water. Especially favors dense thickets and oaks in secluded canyons near streams.

NEST: Nearly always places nest on the ground under a rock, tree root, or grass tuft that provides overhead shelter, and usually on a sloping bank or rocky canyon wall near water.

FOOD: Gleans its food from leaves, tree trunks, and branches. Also hovers while picking insects from tree foliage, and hawks over water. Mostly eats insects. (Food habits have not been reported, however.)

REFERENCES: Bent 1953b, Griscom and Sprunt 1979, Marshall and Balda 1974, Oberholser 1974b.

Yellow-breasted Chat

Icteria virens

L 6¼"



RANGE: Breeds from southern British Columbia, North Dakota, southern Minnesota, southern Ontario, Vermont, and New Hampshire south to south-central Baja California, the Gulf Coast, north-central Florida, and Mexico. Winters from southern Texas and southern Florida south through Central America and western Panama.

STATUS: Common.

HABITAT: Favors ravine or streamside thickets of vines, briars, small trees, and tall shrubs. Also inhabits forest edges, hedgerows, overgrown pastures, scrub country, and early successional stages of forest regeneration.

SPECIAL HABITAT REQUIREMENTS: Dense shrubs and vines with scattered young trees.

NEST: Usually builds nest 2 to 8 feet above the ground in dense small bushes, vines, or briars. May sometimes nest in groups or colonies, but maintains separate territories.

FOOD: Primarily eats insects gleaned from foliage and shrub stems; also eats some berries and fruits.

REFERENCES: Bent 1953b, Dennis 1958, Griscom and Sprunt 1979, Petrides 1938, Thompson and Nolan 1973.

Olive Warbler

Peucedramus taeniatus



RANGE: Breeds from central and southeastern Arizona and southwestern New Mexico through the highlands of Mexico to north-central Nicaragua. Winters throughout the breeding range, except in Arizona and New Mexico, where it moves southward.

STATUS: Fairly common.

HABITAT: Generally found near the summits of mountains in the Southwest above 8,000 feet in mixed pine-fir forests; usually observed near the tops of coniferous trees.

NEST: Builds a cup-shaped nest, usually placed on the limb of a conifer tree limb near the end, sometimes hidden by pine needles or a cluster of mistletoe; usually high (30 to 80 feet) above the ground.

FOOD: Spends considerable time creeping over the branches and twigs of pines searching for insects. (No studies on food habits have been reported.)

REFERENCES: Bent 1953a, Griscom and Sprunt 1979.

Hepatic Tanager

Piranga flava



RANGE: Breeds from southeastern California and northwestern Arizona through New Mexico and the Trans-Pecos region of Texas, south through the highlands of Mexico and Central America to central Argentina. Winters from northern Mexico through the breeding range; casually in southern California and southern Arizona in winter.

STATUS: Fairly common.

HABITAT: Generally favors dense pine and pine-oak woodlands between 5,000 and 7,500 feet in elevation, but also inhabits the more monotypic pine, oak, and pinyon-juniper woodlands near streams.

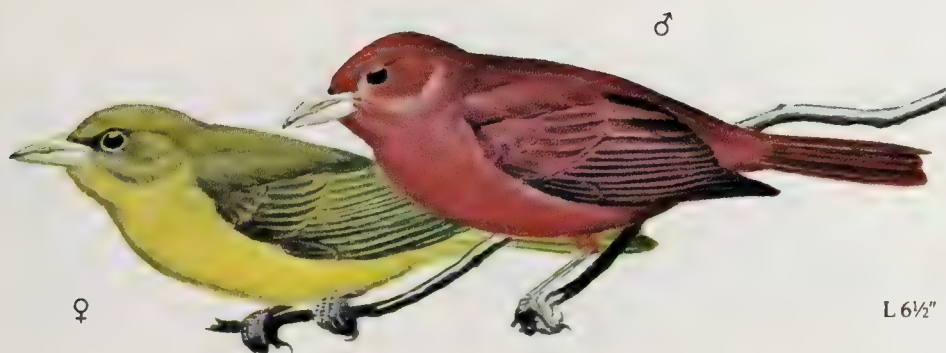
NEST: Builds a flat, saucer-shaped nest, usually in a fork near the end of a horizontal tree branch, 15 to 50 feet above the ground.

FOOD: Gleans insects from branches and leaves of oaks and pines. It occasionally hawks for flying insects, and during the summer eats some fruits. (No studies of food habits have been reported.)

REFERENCES: Bent 1958, Phillips et al. 1964, Terrill in Farrand 1983c.

Summer Tanager

Piranga rubra



RANGE: Breeds from southeastern California and southern Nevada to central Oklahoma, and from southeastern Nebraska to New Jersey south to the Gulf Coast and northern Mexico. Winters mainly from Mexico to Bolivia; rare winter visitor in southern temperate areas.

STATUS: Common.

HABITAT: Generally inhabits dry, open woodlands of oaks, pines, and hickories in the Southeast; but only rich bottomland forests at the northern edge of its range. Inhabits low-elevation willows and cottonwoods, and streamside vegetation in canyons in the Southwest.

NEST: Builds a flimsy, flat, shallow cup nest on a horizontal limb (often oak) 10 to 35 feet above the ground.

FOOD: Eats many bees and wasps, and the larvae from wasp nests. Catches insects in the air and also eats some small fruits. (Food habits have not been thoroughly studied.)

REFERENCES: Bent 1958, Fitch and Fitch 1955, Forbush and May 1955, Johnsgard 1979, Potter 1973, Terres 1980.

Scarlet Tanager

Piranga olivacea



RANGE: Breeds from southern Manitoba, western Ontario, southern Quebec, and New Brunswick south to eastern North Dakota, central Nebraska, southern Kansas, eastern Oklahoma, central Arkansas, northern Alabama, and northern Georgia; casually in the West. Winters in South America.

STATUS: Common.

HABITAT: Generally inhabits mature deciduous and mixed deciduous-coniferous woodlands, roadside shade trees, wooded parks, and large shade trees of suburbs. In the Great Plains, primarily inhabits mature hardwood forests of river valleys, hillsides, and valleys.

SPECIAL HABITAT REQUIREMENTS: Mature deciduous or mixed woodlands.

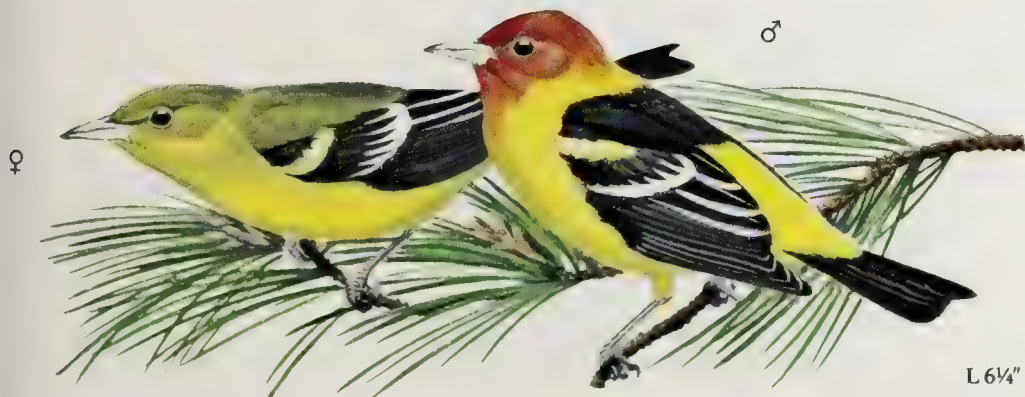
NEST: Builds a shallow, saucer-shaped nest, usually well out on a horizontal limb of a large tree, usually in a leaf cluster or in a position where it is shaded from above.

FOOD: Gleans food from tree tops, shrubs, or the ground. Eats a great variety of insects, slugs, snails, worms, spiders, and millipedes; also some wild fruits.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Terres 1980, Vickery in Farrand 1983c.

Western Tanager

Piranga ludoviciana



RANGE: Breeds from southeastern Alaska, northern British Columbia, southern Mackenzie, northern Alberta, and central Saskatchewan south to northern Baja California, southern Nevada, southwestern Utah, central and southeastern Arizona, southern New Mexico, and western Texas, and east to eastern Montana, western South Dakota, northwestern Nebraska, central Colorado, and central New Mexico. Winters from Baja California and central Mexico south to Central America.

STATUS: Common.

HABITAT: Generally inhabits relatively open, mature coniferous forests up to 10,000 feet in elevation. Breeds less frequently in mixed forests and in deciduous forests in the mountains, along rivers, or in gulches and canyons at lower elevations.

NEST: Builds a shallow, compact, saucer-shaped nest, saddled in a fork of a horizontal branch well out from the trunk. Usually locates nest in a coniferous tree.

FOOD: Consumes insects gleaned from foliage or branches or caught while hawking (about 82 percent of the diet) and fruits (about 18 percent).

REFERENCES: Beal 1907 in Bent 1958, Johnsgard 1979, Harrison 1979.

Northern Cardinal

Cardinalis cardinalis



L 7¼"

RANGE: Resident from southeastern South Dakota, central Minnesota, northern Wisconsin, and southern Ontario to Massachusetts and Nova Scotia, south to the Gulf Coast and southern Florida. Local in southwestern Texas and New Mexico, southern Arizona, and southeastern California south throughout the Mexican lowlands.

STATUS: Common in most of the eastern range; local in the Southwest.

HABITAT: Inhabits forest edges or brushy forest openings, parks, and residential areas with shrubs and low trees, second-growth woods, and open swamps. In the Southwest, inhabits brushy habitats of washes, riparian and residential areas, and the denser desert thorn-scrub.

SPECIAL HABITAT REQUIREMENTS: Dense forest understory or dense shrub habitat.

NEST: Builds a loose nest in dense shrubbery, small deciduous or coniferous trees, thickets, vines, briar tangles, or mesquite trees, generally less than 10 feet, but may be up to 20 feet, above the ground.

FOOD: Primarily eats vegetable matter gleaned from the ground, including grains, miscellaneous weed seeds, and wild fruits. Also eats smaller amounts of insects.

REFERENCES: Forbush and May 1955, Harrison 1979, Johnsgard 1979, McAtee 1908, Terrill in Farrand 1980.

Pyrrhuloxia

Cardinalis sinuatus



RANGE: Resident from Baja California, south-central and southeastern Arizona, southern New Mexico, and southern and western Texas south to central Mexico.

STATUS: Fairly common.

HABITAT: Generally lives yearlong in thorny thickets, especially at the edges of mesquite along desert arroyos, in thorny shrubs at lower, wide mouths of mountain canyons, and in thickets along streams. In winter, often wanders from thickets to feed in flocks along roads, fencerows, and borders of fields.

NEST: Builds a compact nest, usually low (3 to 8 feet above the ground), in a thorny shrub or tree, or in a clump of mistletoe.

FOOD: Gleans most of its food from the ground. During the winter, eats cactus fruits, seeds of grasses, weeds, and mesquite, and catkins of cottonwood. In summer, also eats insects.

REFERENCES: Harrison 1979, Oberholser 1974b, Terres 1980.

Rose-breasted Grosbeak

Pheucticus ludovicianus



RANGE: Breeds from southern Mackenzie, across southern Canada to Nova Scotia south to north-central North Dakota and Kansas, central Oklahoma, southern Missouri, central Indiana and Ohio to central New Jersey and south along the Appalachians to northern Georgia. Winters from central Mexico to South America; rare in the Southwest.

STATUS: Common.

HABITAT: Seems to require a combination of large trees, open areas, and thick shrubs or brush. In summer, inhabits second-growth deciduous or mixed woods, borders of swamps and streams, dense growths of small trees and shrubs along edges of woods and pastures, gardens, and parks of towns and villages.

SPECIAL HABITAT REQUIREMENTS: Forest edges with dense brush or thick sapling stands.

NEST: Builds a flimsy nest, usually in a fork of a deciduous tree or shrub, about 10 to 15 feet above the ground. Occasionally builds nest in conifer trees.

FOOD: Consumes about equal amounts of vegetable and animal matter gleaned from leaves, twigs, or from the ground. Vegetable matter includes weed seeds, fruit, and tree seeds and buds; animal portion is nearly all insects.

REFERENCES: Forbush and May 1955, Harrison 1975, McAtee 1908, Terres 1980, Vickery in Farrand 1983c.

Black-headed Grosbeak

Pheucticus melanocephalus



L 7¼"

RANGE: Breeds from southern British Columbia east to southern Saskatchewan and central Kansas south to southern Mexico. Winters mainly in western Mexico from southern Baja California and southern Sonora south to Oaxaca. Rare in the Southwest during winter.

STATUS: Common.

HABITAT: Primarily inhabits relatively open stands of deciduous forests in uplands or floodplains, but also found in or near orchards, brushy woodlands or chaparral, edges or transitions between grasslands and woodlands, riparian groves or thickets, and parks or suburbs with many trees.

NEST: Builds a bulky, open-cup nest 4 to 12 feet above the ground in a fork of a variety of shrubs or small trees. Mostly nests (about 80 percent) in deciduous trees and shrubs.

FOOD: Gleans food from leaves, stems, or the ground. Mostly (about 57 percent) eats animal material (mainly spiders and insects); also eats vegetable foods (seeds and fruits.)

REFERENCES: Bent 1968a, Bevier in Farrand 1983c, Johnsgard 1979, Terres 1980, Weston 1947.

Blue Grosbeak

Guiraca caerulea



RANGE: Breeds from southern California, southern Nevada, southern Colorado, and Nebraska (also north to south-central North Dakota) and southern Ohio and New Jersey south to the Gulf Coast, and central Florida, through Mexico into Costa Rica. Winters from Mexico south to Panama, and in the Bahamas and Cuba.

STATUS: Fairly common, but rare and local in the northeastern part of its range.

HABITAT: Inhabits weedy pastures, old fields with saplings, forest edges, streamside thickets, hedgerows, swampy thickets, and willows along irrigation ditches. In the West, inhabits mesquite woods.

NEST: Builds a compact, rather deep nest 3 to 8 feet above the ground in a low tree, shrub, tangle of vines, or briars, and typically at the edge of an open area.

FOOD: Gleans much of its food from the ground, but also searches for food among leaves and branches of trees and shrubs. Consumes insects, snails, spiders, grain, weed seeds, and fruits.

REFERENCES: Forbush and May 1955, Johnsgard 1979, Stabler 1959, Terres 1980.

Lazuli Bunting

Passerina amoena



L 4½"

RANGE: Breeds from southern British Columbia to central North Dakota and northeastern South Dakota south to northwestern Baja California, southern Nevada, central Arizona, central New Mexico, and central Texas. Winters from southern Baja California and southern Arizona south to Guerrero and central Veracruz.

STATUS: Common to uncommon.

HABITAT: Inhabits a variety of habitats from near sea level to 10,000 feet in the Sierras and 8,000 feet in the Rocky Mountains of Colorado. Generally found in diverse habitats with an abundance of shrubs, low trees, and herbaceous vegetation such as thicketed swales and draws of prairies and dry bushy hillsides, wooded valleys, aspen groves, and shrubby banks of mountain streams. In much of the arid West, found in riparian vegetation.

SPECIAL HABITAT REQUIREMENTS: Shrubby vegetation.

NEST: Builds a coarsely woven cup nest attached to supporting stalks or a fork of a low shrub or vine tangle, usually 2 to 4 feet above the ground.

FOOD: Forages on or near the ground in shrubs and occasionally hawks for insects. Consumes animal material (primarily insects which account for over half of the spring and summer diet) and grass and weed seeds.

REFERENCES: Bent 1968a, Grinnell and Miller 1944, Harrison 1979, Johnsgard 1979, Terres 1980.

Indigo Bunting

Passerina cyanea



L 4½"

RANGE: Breeds from southeastern Saskatchewan and northern Minnesota to southern New Brunswick, south to southern New Mexico, central and southeastern Texas, the Gulf Coast, and central Florida; locally in central Colorado, southwest Utah, central Arizona, and southern California. Winters primarily in southern Mexico, Cuba, and the West Indies south to Panama; also in southern Florida and infrequently in coastal Texas.

STATUS: Common in eastern range.

HABITAT: Generally associated with edges of woods, old burns, open brushy fields, roadside thickets, and brushy ravines. Tends to be more numerous along streams, and avoids deep woods.

SPECIAL HABITAT REQUIREMENTS: Forest edges.

NEST: Builds a cup nest 1 to 12 feet above the ground in a crotch of a bush, shrub, or low tree, in a tangle of berry vines, or in canebrakes. Frequently parasitized by brown-headed cowbird.

FOOD: Forages on or near the ground in shrubs, and eats a variety of foods, including insects, weed seeds, berries, and fruits.

REFERENCES: Bent 1968a, DeGraff et al. 1980, Forbush and May 1955, Harrison 1975.

Varied Bunting

Passerina versicolor



RANGE: Breeds in south-central and southeastern Arizona, southwestern and southeastern New Mexico and southern Texas south to Mexico and Guatemala. Winters from southern Texas south throughout the breeding range.

STATUS: Local and uncommon.

HABITAT: Inhabits mesquite or thorny shrubs, brushy pastures, dense vegetation with few cottonwoods, foothill canyons, and generally hilly and rocky terrain; tends to avoid heavily wooded areas.

SPECIAL HABITAT REQUIREMENTS: Thorny shrubs.

NEST: Builds a compact cup nest 2 to 10 feet above the ground in the crotch of a shrub, low tree, or vine tangle.

FOOD: Presumably eats insects and seeds similar to the diet of the indigo and lazuli buntings. (No definitive studies have been made.)

REFERENCES: Bent 1968a, Harrison 1979, Oberholser 1974b, Terres 1980.

Painted Bunting

Passerina ciris



L 4½"

RANGE: Breeds from southeastern New Mexico and southern Missouri south to southern Alabama and into Mexico, also along Atlantic Coast from southeast North Carolina south to central Florida. Winters from southeastern Texas, central Florida, the Bahamas, and Cuba south through Mexico to Panama.

STATUS: Locally common.

HABITAT: Inhabits open country with brushy and weedy fields, hedges, edges of woods, roadside shrubs, gullies, thickets along streambanks, shelterbelts, and gardens.

NEST: Nests in a variety of deciduous shrubs, small trees, and vines. Attaches shallow cup nest to twigs or other supporting vegetation, 3 to 9 feet above the ground, in bushes, low trees, or vine tangles. Raises two and sometimes three broods each year; susceptible to parasitism by brown-headed cowbirds.

FOOD: Mostly eats vegetable matter, which is gleaned from the ground or seed heads of grass, but also some animal matter (insects and a few spiders.)

REFERENCES: Bent 1968a, Harrison 1979, Johnsgard 1979, Sykes in Farrand 1983c, Terres 1980.

Dickcissel

Spiza americana



RANGE: Breeds from eastern Montana and southern Canada to Massachusetts, south to central Colorado, southern Texas, and central South Carolina. In the eastern portion of the range, breeds sporadically and irregularly. Winters mostly from Mexico to northern South America. Winters locally (in small numbers) in coastal lowlands from southern New England south to Florida and west to southern Texas.

STATUS: Common in the Plains, but rare and local in the East; overall population appears to be declining.

HABITAT: Generally inhabits grasslands having tall grasses, forbs, or shrubs but also fields planted to such crops as alfalfa, clover, and timothy. Also frequents abandoned or fallow croplands.

SPECIAL HABITAT REQUIREMENTS: Dense herbaceous cover and song perches.

NEST: Builds a bulky, cup nest on the ground or attached to forks in shrubs, vines, or low trees. Locates nests in a variety of situations such as marshes, hayfields, abandoned or fallow croplands, roadsides, fencerows, and grasslands.

FOOD: Gleans most of its food from the ground; eats mainly vegetable materials — weed seeds and grain, and some insects.

REFERENCES: Harmeson 1974, Gross 1921, Overmire 1962, Taber 1947, Tate and Tate 1982, Zimmerman 1982.

Olive Sparrow

Arremonops rufivirgatus



RANGE: Resident in south Texas and south locally to Costa Rica.

STATUS: Fairly common locally.

HABITAT: Generally inhabits thorny shrub habitats such as mesquite, ebony blackbead, anacua, huisache, and retaima in the Rio Grande delta. Farther north, found in streamside cane, briars, willows, ash, and live oaks.

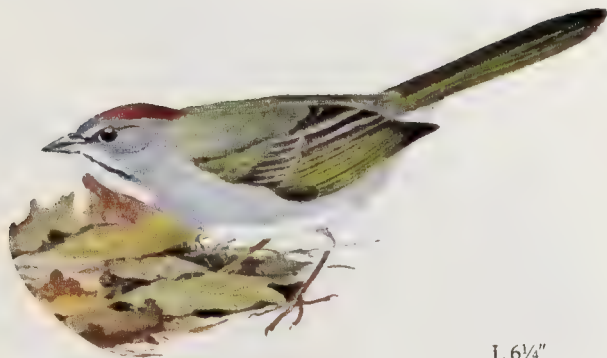
NEST: Builds a domed or nearly round nest 2 to 5 feet above the ground in tangles of shrubbery, pricklypear, or low shrubs, usually near the center of the plant.

FOOD: Forages on the ground scratching for insects and various seeds. (Little has been reported on food habits.)

REFERENCES: Bent 1968a, Harrison 1979, Oberholser 1974b.

Green-tailed Towhee

Pipilo chlorurus



L 6¼"

RANGE: Breeds from southeastern Washington, southern Idaho, southwestern Montana, northwestern and southeastern Wyoming south through the interior mountains to southern California, southern Nevada, and central Arizona to western Texas. Winters from southern California to western and southern Texas south to central Mexico; casual east of the breeding range in fall and winter.

STATUS: Fairly common.

HABITAT: Generally inhabits relatively arid and brushy foothills with shrubs such as sagebrush, deerbrush, snowbrush, wild rose, spirea, manzanita, waxberry, and chokecherry, from 2,500 feet elevation in California to 10,500 feet in Arizona. Tends to breed at higher elevations in the south than in the north.

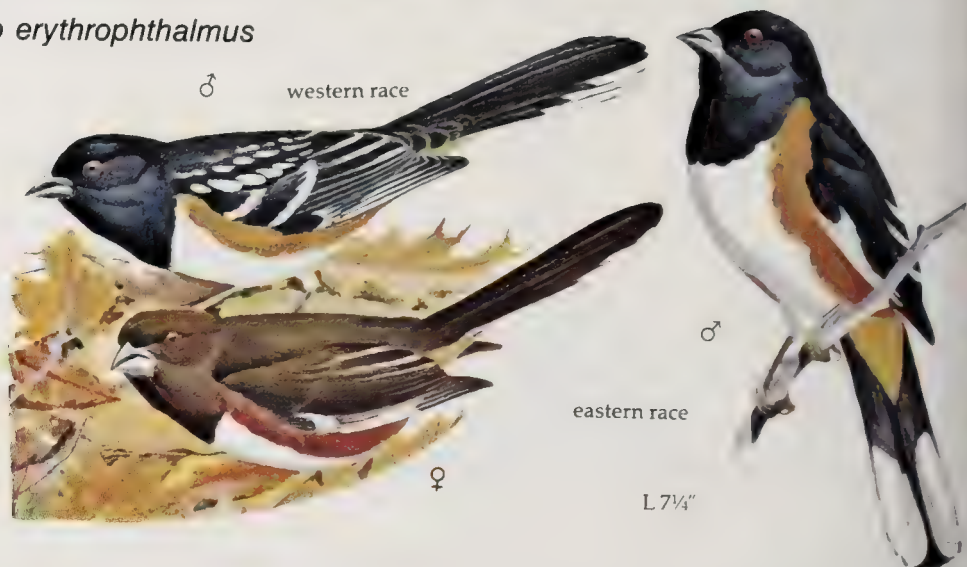
NEST: Builds a large, loosely constructed and deeply cupped nest on the ground or in low shrubs such as sagebrush, waxberry, and snowbrush, usually less than 2 feet above the ground.

FOOD: Forages on the ground, and eats berries, weed seeds, and insects. (Food habits studies are limited.)

REFERENCES: Bent 1968a, Harrison 1979, Johnsgard 1979.

Rufous-sided Towhee

Pipilo erythrophthalmus



RANGE: Breeds from southern British Columbia to southern Maine south to southern Baja California, Guatemala, northern Oklahoma, eastern Louisiana, and southern Florida. Winters from southern British Columbia, Utah, Colorado, the southern Great Lakes area, and along the Atlantic Coast south throughout the breeding range.

STATUS: Common and widespread.

HABITAT: Generally inhabits dense brushy fields and pastures, edges of woods, open woodlands, hedgerows, roadside thickets, and clearings. In the West, inhabits sagebrush, willows, and chaparral above the deserts.

SPECIAL HABITAT REQUIREMENTS: Dense brushy cover.

NEST: Builds a bulky nest, usually in a depression in the ground but sometimes up to 3 feet above the ground in low shrubs such as coffeeberry or sagebrush. Conceals and protects nest with overhanging bushes, logs, vines, or a clump of grass.

FOOD: Mostly eats vegetable material (about 70 percent of diet) gleaned from the ground; most important items are acorns, weed seeds and small fruits. Also eats insects, spiders, and snails.

REFERENCES: Baumann 1959, Bent 1968a, Davis 1960.

Brown Towhee

Pipilo fuscus



L 7¼"

RANGE: Resident from southwestern Oregon, California (except higher mountains, deserts, and extensive forests), Arizona, southeastern Colorado, and west-central Texas south to central and western Mexico.

STATUS: Locally abundant.

HABITAT: Generally inhabits chaparral, brushland, woodlands, and open habitats such as lawns and gardens — chaparral and suburban gardens in Oregon and California; cholla cactus and pinyon-juniper in Colorado; the lower mountain canyons in Arizona; and low scrub habitats in New Mexico and Texas.

SPECIAL HABITAT REQUIREMENTS: Low shrubs.

NEST: Builds a bulky nest ranging from ground level up to 35 feet above the ground (usually 3 to 12 feet) in a variety of shrubs and low trees. Usually places nest in the densest part of the foliage, supported by several branches.

FOOD: Forages on the ground for seeds and insects. Feeds insects to nestlings during summer; eats predominately weed seeds in winter. Also eats grain and small fruits.

REFERENCES: Bent 1968b, Johnsgard 1979, Terres 1980.

Abert's Towhee

Pipilo aberti



L 7¼"

RANGE: Resident from southeastern California, extreme southeastern Nevada, southwestern Utah, central and southeastern Arizona, and southwestern New Mexico south to northeastern Baja California and northwestern Sonora.

STATUS: Common.

HABITAT: Lives yearlong in shrubby vegetation such as willow, cottonwood, mesquite, and arrowweed, usually near water courses. Less commonly inhabits baccharis and tamarisk, citrus groves, farms, and urban areas.

SPECIAL HABITAT REQUIREMENTS: Riparian shrubs.

NEST: Builds a bulky nest, usually near the ground in low shrubs such as mesquite, elder, ash, umbrella trees, or arrowweed; occasionally in trees up to 30 feet above the ground.

FOOD: Apparently scratches in leaves on the ground, searching for seeds and insects. (No comprehensive study of food habits has been published.)

REFERENCES: Bent 1968b, Phillips et al. 1964, Terres 1980.

White-collared Seedeater

Sporophila torqueola



RANGE: Resident from southern Texas (the Rio Grand Valley north to Webb County), and northern Mexico south to Panama.

STATUS: Rare and irregular in Texas.

HABITAT: Generally prefers open, grassy places including pastures, roadsides, weedy fields, or marshlands covered with tall grasses in the vicinity of low-growing shrubs such as huisache or retaima.

NEST: Builds a delicate cup nest 3 to 5 feet above the ground in crotches of weeds or low shrubs. Frequently nests in abandoned weedy fields, often in giant ragweed.

FOOD: Generally forages among low shrubs and weeds to glean seeds of grasses and forbs; also eats some insects. (Little has been reported on its food habits.)

REFERENCES: Bent 1968a, Oberholser 1974b.

Bachman's Sparrow

Aimophila aestivalis



L 5½"

RANGE: Breeds from south-central Missouri and central Indiana to central Maryland, south to eastern Texas, the Gulf Coast, and south-central Florida. Winters from eastern Texas, the Gulf States, and southeastern North Carolina south through the breeding range.

STATUS: Uncommon and local, with the population down over most of its range.

HABITAT: Generally favors brushy hillsides or wooded borders in the northern part of its range, and open pine stands with grasses and scattered shrubs, oaks, or other hardwoods in more southern areas. Inhabits pine barrens in South Carolina, grassy fields in Mississippi, grasslands with scattered young pines and blackberry thickets in Oklahoma, open pine stands in Florida, and limestone glades in Missouri.

SPECIAL HABITAT REQUIREMENTS: Dense herbaceous cover interspersed with, or bordered by, shrubs and trees.

NEST: Constructs a well-concealed nest (open or domed) on the ground, usually under a low bush or against a tussock of grass, and often located at the outer edges of grass clumps in slight depressions, with a clear view in front of the nest.

FOOD: Forages on the ground primarily for insects and spiders, but also consumes seeds of a variety of plants.

REFERENCES: Hardin et al. 1982, Johnsgard 1979, Tate and Tate 1982, Weston in Bent 1968b.

Botteri's Sparrow

Amimophila botterii



L 5½"

RANGE: Breeds from southeastern Arizona and extreme southern Texas south to Costa Rica. Winters from northern Mexico south throughout the breeding range.

STATUS: Rare and local.

HABITAT: Only inhabits areas with dense, tall grass, breeding in open grassland and savannah, especially in areas with scattered brush or shrubs. Favors tall grass habitats with mesquite and catclaw in Arizona; prefers salt-grass with some yucca, pricklypear, and mesquite in the coastal prairies of Texas.

SPECIAL HABITAT REQUIREMENTS: Open grassland with scattered shrubs or small trees.

NEST: Builds nest on the ground among tall grasses, at the base of a tuft of grass, or sometimes under a projecting mat of grass.

FOOD: Primarily eats insects but also spiders and seeds.

REFERENCES: Cottam and Knappen 1939, Monson in Bent 1968b, Oberholser 1974b, Terrill in Farrand 1983c.

Cassin's Sparrow

Aimophila cassinii



L 5½"

RANGE: Breeds from southeastern Arizona, New Mexico, central and northeastern Colorado, southwestern Nebraska, and Kansas south into Mexico and Texas. Singing males may appear sporadically from southern California to South Dakota. Winters from southeastern Arizona and western and south-central Texas into Mexico.

STATUS: Common.

HABITAT: Prefers open grassland and short-grass plains with a few scattered shrubs or small trees. Also frequents mesquite grasslands if the mesquites are small with open areas throughout but will not usually inhabit areas that are entirely grass unless surrounded by a fence for perching. Occasionally occurs in or near mountainous areas, on grassy slopes with scattered yuccas or small oaks. Favors sandy prairies with scattered sage, yucca, cactus, mesquite, and shinnery oaks in Oklahoma. Apparently can breed where no drinking water is available locally.

SPECIAL HABITAT REQUIREMENTS: Short-grass plains with scattered shrubs.

NEST: May nest either on the ground, or up to 12 inches above the ground in low bushes or among tangled branches of cacti. Typically places ground nests at the foot of small shrubby plants, concealed in weeds or placed in a tuft of grass.

FOOD: Eats mainly insects taken from the ground or the grass. In the winter, eats small seeds of weeds and grasses.

REFERENCES: Johnsgard 1979, Williams and LeSassier in Bent 1968b.

Rufous-winged Sparrow

Amphispiza bilineata



L 5¼"

RANGE: Resident from south-central Arizona south into Mexico.

STATUS: Locally common.

HABITAT: Occurs in rather restricted, isolated colonies in open flat grassy areas with scattered thorn bushes, bunch grasses, mesquite, or cholla. Inhabits desert swales with wide grassy bottoms, leguminous brush, and low trees, washes with sandy bottoms but vegetated slopes; creeks bordered by broad-leaved trees, mesquite, grasses, and weeds; and brushy irrigation ditches.

SPECIAL HABITAT REQUIREMENTS: Grassy areas with scattered shrubs that are thorny or dense, preferably both.

NEST: Nests in the edges of bushes such as hackberry, paloverde, cholla cacti, or mesquite, usually in a crotch or fork of a branch, 5 to 10 feet above the ground. Also will nest in dense clumps of mistletoe.

FOOD: During the nesting season, feeds on a variety of insects caught on the wing or gleaned from plant surfaces. During other seasons, presumably eats grass and weed seeds.

REFERENCES: Phillips in Bent 1968b, Phillips et al. 1964, Terres 1980, Terrill in Farrand 1983c.

Rufous-crowned Sparrow

Aimophila ruficeps



RANGE: Breeds from central California, southwestern Utah, southeastern Colorado, and central Oklahoma south into Mexico. Winters from north-eastern New Mexico, northern Texas, and south-central Oklahoma south throughout the breeding range.

STATUS: Locally common.

HABITAT: Inhabits dry and desertlike habitats, preferring rocky, brushy, relatively arid hillsides with extensive bare areas. Also in rocky glades on the Great Plains; low ridges and foothills covered with scattered shrubs or trees and grass in Arizona; rocky slopes with large boulders, small cedars, and stunted oaks in Oklahoma; and grassy hillsides with scattered rocks and shrubs, especially sagebrush, and coastal scrub in California.

SPECIAL HABITAT REQUIREMENTS: Rocky, arid slopes with scattered brush and grass.

NEST: Usually builds nest in a small depression on the ground, often near or under a clump of grass, or at the base of a shrub or small tree. Also locates nests up to 2 feet above ground, wedged among dense verticle growing branches in shrubs and low trees.

FOOD: During the nesting season, feeds on a variety of insects and some spiders caught while foraging on or near the ground. In other seasons, eats some seeds.

REFERENCES: Cogswell in Bent 1968b, Johnsgard 1979, Phillips in Bent 1968b, Terres 1980, Terrill in Farrand 1983c, Verner and Boss 1980.

American Tree Sparrow

Spizella arborea



RANGE: Breeds from Alaska and northern Yukon across Canada to northern Quebec and Labrador, and south to northwestern British Columbia, northern Saskatchewan, and central Quebec. Winters from southern Canada south to northern California, northern and east-central Arizona, north-central Texas, Arkansas, and North Carolina.

STATUS: Common.

HABITAT: During the nesting season, inhabits scrub conifers, boggy meadows, and wet, hummocky tundra strewn with boulders and interspersed with willow, birch scrub, and other low shrubbery. Occurs as far north as scrubby growth is found, and in sparse forests just below treeline. In winter, frequents open country, weedy fields, brushy pastures, marshes, fencerows, hedgerows, and thickets.

SPECIAL HABITAT REQUIREMENTS: Scrubby trees or bushes for nesting.

NEST: Usually constructs nest on or near the ground in a depression, in a tussock of grass, or atop a mossy hummock, placed at the base of a tree or shrub, and concealed by grasses. Occasionally, places nest up to 5 feet above ground in dwarf spruce or willow.

FOOD: In summer, primarily eats insects plus some plant material, while in winter, primarily eats seeds of weeds and grasses.

REFERENCES: Baumgartner 1937a, 1937b; Bent 1968b; DeGraff et al. 1980; Forbush and May 1955.

Chipping Sparrow

Spizella passerina



L 4¾"

RANGE: Breeds from east-central and southeastern Alaska and central Yukon to northern Manitoba, southern Quebec, and southwestern Newfoundland south to southwestern and east-central California, central and eastern Texas, the Gulf Coast, and northwestern Florida through the highlands of Mexico to Nicaragua. Winters from central California, northern Texas, Tennessee, and Maryland south in Mexico throughout the breeding range.

STATUS: Common.

HABITAT: Inhabits gardens, residential areas, farms, orchards, open coniferous and deciduous woodlands, forest edges and clearings, wooded borders of lakes and rivers, mountain meadows, and grassland habitats with scattered trees. Prefers habitats with trees surrounded by an open area with only herbaceous vegetation and some open ground for foraging. In winter, favors weedy fields and dry scrubland.

NEST: Builds nest 1 to 25 feet, but usually 3 to 10 feet, above ground in trees, especially conifers, shrubs, or vines. Generally locates nest near the trunk and top of smaller trees, or lower in the branches and farther from the trunk in larger open-grown trees, usually well concealed.

FOOD: Generally forages on the ground in open meadows or lawnlike areas gleaning insects and seeds.

REFERENCES: Beal and McAtee 1912, DeGraff et al. 1980. DeSante in Farrand 1983c, Forbush and May 1955, Johnsgard 1979, Johnson in Bent 1968b, Stull in Bent 1968b, Walkinshaw 1944.

Clay-colored Sparrow

Spizella pallida



L 4½"

RANGE: Breeds from eastern British Columbia and west-central and southern Mackenzie east to central Ontario, and south to eastern Washington, central Montana, eastern Colorado, northern Iowa, central and southeastern Michigan, and southwestern Quebec. Winters from central Texas to southern Mexico.

STATUS: Locally common.

HABITAT: Prefers midwestern mixed-grass prairies with scattered low thickets of shrubs such as wolfberry; will inhabit a variety of dry, uncultivated shrubby habitats, including grasslands with taller shrubs or small trees, brushy hillsides, overgrown clearings and pastures, parklands, brushy woodland edges, burned-over areas, weedy thickets along roads, swamps, fencerows, railroad tracks and fields, shelterbelts, and other early successional disturbed habitats.

SPECIAL HABITAT REQUIREMENTS: Open brushland.

NEST: Builds nest either on the ground, well hidden in a tuft of grass at the base of a shrub or near a clump of weeds, or up to 4 1/2 feet above ground in a low shrub or small tree. Commonly uses snowberry, rosebushes, serviceberry, and conifers for nesting.

FOOD: Feeds primarily on a wide variety of weed and grass seeds, but will also eat insects in spring and summer, and willow catkins and the buds of elms and other trees in spring.

REFERENCES: Forbush and May 1955, Fox 1961, Hussong 1946, Johnsgard 1979, Knapton 1978, Root in Bent 1968b, Salt 1966.

Brewer's Sparrow

Spizella breweri



L 4½"

RANGE: Breeds from southwestern Yukon and northwestern interior British Columbia to southwestern Saskatchewan south, generally east of the Cascades and coast range, to southern California, central Arizona, central Colorado, and southwestern South Dakota. Winters from southern interior California to central Texas south into Mexico.

STATUS: Common.

HABITAT: Inhabits open, shrub-dominated habitats; arid sagebrush country in the West and scrub balsam-willow habitats in timberline areas of western Canada, as well as bunchgrass prairie with rabbitbrush, dry, brushy mountain meadows, and pinyon-juniper woodlands.

SPECIAL HABITAT REQUIREMENTS: Exposed scrub vegetation from desert regions in the south to timberline in Canada.

NEST: Builds nest in shrubs, especially sagebrush, almost always located less than 4 feet above the ground. At timberline, locates nest 6 inches above ground in birch trees, well concealed overhead by interlocking branches. Rarely nests on the ground.

FOOD: During winter, primarily eats weed seeds. In spring and summer, also consumes insects and spiders.

REFERENCES: Paine in Bent 1968b, Reynolds 1981.

Field Sparrow

izella pusilla



L 5"

RANGE: Breeds from northwestern and southeastern Montana and northern North Dakota to southwestern Quebec and southern New Brunswick south to western Kansas, southern Texas, the Gulf Coast, and southern Georgia. Winters from Kansas to Massachusetts, and south to Mexico, the Gulf Coast, and southern Florida.

STATUS: Common.

HABITAT: Occurs in a variety of habitats that provide low grassy areas and shrubs or low trees, including old fields and pastures overgrown with briar thickets or deciduous underbrush, brushy fencerows, cut over pine forests and burned-over woodlands wherever briars and brush have regenerated, edges of open, unplowed fields, sagebrush flats, forest edges, and other similar habitats.

SPECIAL HABITAT REQUIREMENTS: Abandoned fields or other open areas with low shrubs or trees.

NEST: Early in the nesting season, usually builds nest on or near the ground in weed clumps or tufts of grass; later in nesting season, builds nest as high as 4 feet above the ground in shrubs or small trees. Occupies nest in a wide range of plant species — grapevines, cinquefoil, blackberry bushes, boxelders, small oaks, and hickories.

FOOD: Gleans a variety of seeds of weeds and grasses from the ground throughout the year; in summer, also eats insects (40 percent of diet.)

REFERENCES: Best 1977, 1978, DeGraff et al. 1980, Forbush and May 1955, Fretwell 1968, Johnsgard 1979, Vickery in Farrand 1983c, Walkinshaw in Bent 1968b.

Black-chinned Sparrow

Spizella atrogularis



RANGE: Breeds from south-central California east to southern Nevada and southwest Utah, south to Arizona, New Mexico, western Texas, and Mexico. Winters from coastal California, southern Arizona, New Mexico, and Texas, south into Baja California and Mexico.

STATUS: Uncommon.

HABITAT: In desert regions, inhabits tall, dense sagebrush or other brushland areas covered with a variety of plant species. Prefers slopes with rocky outcrops and scattered pinyon or juniper trees. In the Far West, inhabits dry chaparral habitat with a variety of shrubs and scrub oak.

SPECIAL HABITAT REQUIREMENTS: Chaparral and sage habitat with rocky outcrops.

NEST: Generally builds a compact cup nest of dry grasses, often lined with animal hair, typically placed at the base of a shrub or in the lower portions of sage and shrub, occasionally up to 40 inches above the ground.

FOOD: Forages through sage and chaparral habitat, presumably taking a variety of seeds, berries, and soft-bodied insects. (Only limited information is available on its food habits.)

REFERENCES: Phillips et al. 1964.

Vesper Sparrow

Pooecetes gramineus



L 5½"

RANGE: Breeds from southern Mackenzie and central Saskatchewan to southern Quebec and Nova Scotia, south to eastern and southern California, central New Mexico, Kansas, and North Carolina. Winters from central California, central Texas, southern Illinois, and Connecticut south to Mexico, the Gulf Coast, and central Florida.

STATUS: Fairly common.

HABITAT: Favors sparsely vegetated dry uplands but also occurs in a variety of habitats throughout its range. In the West, inhabits open grasslands and sagebrush flats, pinyon-juniper associations, open meadows and farmlands, and low grassy areas of alpine and subalpine meadows. In the East, inhabits short-grass meadows, pastures, hayfields, country roadsides, prairie edges, blueberry barrens, coastal beachgrass, and, farther north, forest clearings and burned-over areas.

SPECIAL HABITAT REQUIREMENTS: Open areas with short herbaceous vegetation and conspicuous song perches.

NEST: Builds nest in a depression on the ground, frequently near small patches of bare ground, where the vegetation is low and sparse, or at the base of a dirt clod, clump of weeds, or tussock of grass, often well concealed by surrounding live or dead vegetation.

FOOD: Gleans insects and seeds from the ground and from weeds and grasses; also forages on waste grains.

REFERENCES: Berger in Bent 1968b, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, King in Bent 1968b, Vickery in Farrand 1983c.

Lark Sparrow

Chondestes grammacus



L 5 3/4"

RANGE: Breeds from western Oregon and Washington, north into southern Canada, east through the Great Plains to the Missouri River, south throughout the Southwest into Mexico. Winters from central California, southern Arizona, and Texas south to Baja California, throughout Mexico, and in parts of the Gulf Coast up through South Carolina.

STATUS: Common throughout most of its range.

HABITAT: Generally inhabits open prairies and other open lands. In the spring, frequently found along roadsides with grassy vegetation, but prefers open areas with scattered brush and trees. Also inhabits forest edges, cultivated areas, orchards, fields, and savannahs.

SPECIAL HABITAT REQUIREMENTS: Dry fields with scattered bushes or trees or open edge.

NEST: Builds nest either on the ground or in low trees or bushes. Breeds in the open but retires to the borders of open woodlands or brushy areas after the young have hatched.

FOOD: Eats both soft-bodied insects and seeds.

REFERENCES: Forbush and May 1955.

Black-throated Sparrow

Amphispiza bilineata



L 4½"

♂

RANGE: Breeds from southeastern Oregon and northern California, east through the Great Basin, south into Baja California and Mexico. Winters from southern Arizona, New Mexico, and Texas, south into Baja California and Mexico.

STATUS: Common in parts of its range.

HABITAT: Inhabits thinly grassed pastureland with scattered mesquite, yucca, pricklypear, and cholla cacti. Generally found in dry uplands but extends into the depths of Death Valley.

SPECIAL HABITAT REQUIREMENTS: Arid areas with scattered shrubs including cactus, sage, and mesquite.

NEST: Generally conceals nest near the ground in small bushes or a variety of cactus species. Usually locates nest about 12 inches from the ground, fastened among forking branches of the low shrubs. Builds nest with small twigs and fibers of sage, frequently lining it with the fur of animals found in the area, such as rabbits.

FOOD: Eats a variety of insects as well as seeds that are available where it is breeding and wintering. Selects soft-bodied insects. Survives in areas lacking water by eating green vegetation or insects.

REFERENCES: Johnsgard 1979.

Sage Sparrow

Amphispiza belli



L 5"

RANGE: Breeds from central Washington and eastern Oregon, east through the Great Basin into Wyoming and Colorado, south to southern California, Arizona, and New Mexico. Resident from southern California, into Baja California and parts of Arizona. Winters in parts of Arizona, New Mexico, eastern Texas, and northern Mexico.

STATUS: Common in parts of its range.

HABITAT: Prefers sage habitat where sagebrush, saltbush, and chaparral are found. Often found in and among the bushes in the Great Basin region and other dry desert areas.

SPECIAL HABITAT REQUIREMENTS: Sagebrush and chaparral with scattered bushes.

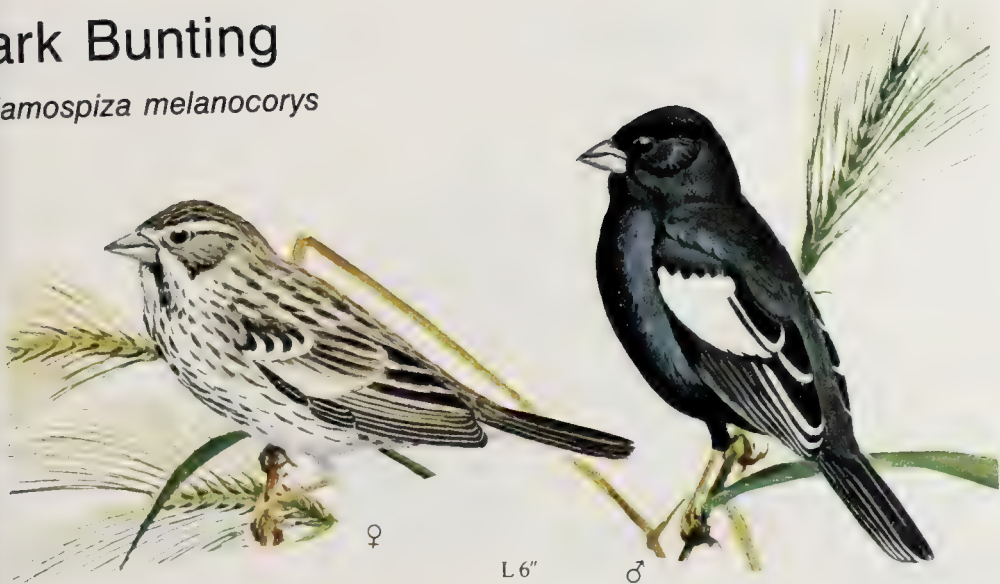
NEST: Usually nests in low shrubs in desert regions, but sometimes in small depressions on the ground. Places nest 6 to 18 inches above the ground, often built into the body of the bush so the foundation is firmly placed. Builds nest of sticks and twigs, often lining it with animal hair and dry grass.

FOOD: Eats soft-bodied insects, ants, and spiders, often obtained from the ground or low in bushes. In winter, primarily eats small seeds and other plant materials.

REFERENCES: Reynolds 1981.

ark Bunting

alamospiza melanocorys



RANGE: Breeds from southern Alberta to southwestern Minnesota, and south, east of the Rockies, to eastern New Mexico, the Texas Panhandle, and northwestern Missouri; also locally or sporadically in southern California and Utah to west-central Texas. Winters from southern California to north-central Texas south into Mexico and southern Louisiana.

STATUS: Common; on the Blue List because of overall declines in population.

HABITAT: On the western Great Plains, inhabits mixed short-grass prairie and other areas of predominately low growth, but also areas of taller grasses with scattered shrubs and disturbed grasslands. Also inhabits sagebrush, fenced pastures, cultivated or fallow alfalfa or clover croplands, weedy roadsides, meadows, and areas of relatively barren ground.

SPECIAL HABITAT REQUIREMENTS: Open habitats with relatively short, herbaceous vegetation.

NEST: Builds nest in a depression in the ground, usually well concealed by grasses or other prairie plants, often located near the base of a plant or plant debris.

FOOD: Feeds on the ground, taking primarily insects during the summer, especially grasshoppers. In other seasons, eats seeds of weeds and grasses predominately.

REFERENCES: Ballard in Farrand 1983c, Baumgartner in Bent 1968b, Forbush and May 1955, Johnsgard 1979, Tate and Tate 1982.

Savannah Sparrow

Passerculus sandwichensis



L 4¾"

RANGE: Breeds from Alaska and northern Yukon to northern Labrador and Newfoundland, south in coastal regions to west-central California, and in the interior to central California, northern New Mexico, Nebraska, Kentucky, and New Jersey. Winters from southern British Columbia and southern Nevada to southern Kentucky and, east of the Appalachians, from Massachusetts south into Mexico. Resident in coastal southern California.

STATUS: Common throughout its range, although the population is down in the western mountains.

HABITAT: Inhabits open wet areas with grass or grasslike vegetation. Occurs in hayfields, pastures, coastal and inland marshes, grassy dunes, wet meadow zones of ponds, lakes, and streams, prairies, open grasslands, bogs, open moist areas of mountain parks and meadows, and tundra.

SPECIAL HABITAT REQUIREMENTS: Dense grassy or herbaceous vegetation of moderate height.

NEST: Places nest in a natural hollow or scratched-out depression in the ground, among thick herbaceous cover, usually well hidden, not only by the dense cover surrounding the nest but also by overhanging vegetation.

FOOD: During summer, mostly eats insects, concentrating primarily on beetles and grasshoppers; also consumes some spiders and snails and gleans a wide variety of seeds.

REFERENCES: Baird in Bent 1968b, DeGraff et al. 1980, Elliott in Bent 1968b, Forbush and May 1955, Johnsgard 1979, Potter 1972, Taber in Bent 1968b, Tate and Tate 1982, Welsh 1975.

Baird's Sparrow

Ammodramus bairdii



L 4½"

RANGE: Breeds from southeastern Alberta to southern Manitoba south to central and eastern Montana, southern South Dakota, and west-central Minnesota. Winters from southeastern Arizona to north-central Texas south into Mexico.

STATUS: Uncommon. Of special concern on the Blue List as population is down on its breeding range.

HABITAT: Favors large areas of prairie grassland with tangles of old and new grasses and patches of shrubs such as snowberry, wolfberry, rose, and willow. Also inhabits ungrazed or lightly grazed mixed-grass prairies, moist meadows, tall-grass prairies associated with wetlands, drier rangelands, fallow and stubble fields, and hayfields. May abandon an area after plowing, burning, mowing, or raking.

SPECIAL HABITAT REQUIREMENTS: Relatively undisturbed or reclaimed grassy prairie with scattered shrubs.

NEST: Nests on the ground, preferably in tall, dense grass or other dense herbaceous vegetation. Places nest in a hollow of a tuft of grass supported by a shrub, well concealed on the ground by overhanging vegetation, or most commonly, in a natural hollow or a shallow excavated depression, with no overhead concealment.

FOOD: Forages on the ground for a variety of seeds throughout the year, but consumes many insects in summer.

REFERENCES: Cartwright et al. 1937, Johnsgard 1979, Lane in Bent 1968b, Tate and Tate 1982.

Grasshopper Sparrow

Ammodramus savannarum



L 4½"

RANGE: Breeds from southern interior British Columbia and southern Alberta to southwestern Quebec and southern Maine south to southern California, central Colorado, northern and south-central Texas, central Georgia, and central North Carolina. Winters from central California (rare) and southern Arizona to Tennessee and North Carolina south to Central America.

STATUS: Common, but population is declining from the Dakotas and Nebraska east to New York and Maryland.

HABITAT: Prefers prairies in the West and cultivated grasslands, especially those with orchardgrass, alfalfa, red clover, and bush clover, in the East. Inhabits mixed-grass, short-grass, and tall-grass prairies, sage prairies, small grain fields and weedy fallow fields. Avoids fields containing more than 35 percent shrubs, but will occupy grassy habitats with some scattered trees.

SPECIAL HABITAT REQUIREMENTS: Continuous tall herbaceous cover and conspicuous song perches.

NEST: Builds nest in a slight depression on the ground, usually well hidden at the base of a clump of grass or other vegetation, with vegetation arched over the top. May nest singly or in small colonies.

FOOD: Gleans food from the ground. Consumes a diet that is 63 percent insects from fall to spring; also includes spiders, snails, and seeds.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Smith 1963, Bent 1968b, Tate and Tate 1980.

Henslow's Sparrow

Ammodramus henslowii



L 4½"

RANGE: Breeds from eastern South Dakota and central Minnesota east to northeastern Massachusetts, and south to central Kansas, northern Kentucky, and east-central North Carolina; also locally in eastern Texas. Winters in coastal states from South Carolina south to Florida, and west to Texas.

STATUS: Uncommon to rare and local. Of special concern on the Blue List due to continued decline in population.

HABITAT: Inhabits meadows and neglected weedy or grassy fields, (often with scattered low bushes) generally preferring situations that are low-lying and damp, but occasionally inhabiting dry or cultivated uplands. Also, inhabits broomsedge fields, old pasturelands, and the drier edges surrounding salt marshes. In winter, frequents grassy openings in pine woods and second-growth woodlands.

SPECIAL HABITAT REQUIREMENTS: Habitats with dense herbaceous vegetation, ground litter, an intermediate moisture range, and singing perches.

NEST: Nests singly or in loose colonies. Places nest in a depression on the ground, at or near the base of a thick grass clump with the base of the nest just above the ground, or 6 to 20 inches above the ground attached to vertical stems of herbaceous vegetation. Conceals nest under overhanging vegetation.

FOOD: During spring, summer, and fall, primarily eats insects (82 percent) and some seeds of weeds and grasses (18 percent) gleaned from the ground.

REFERENCES: Forbush and May 1955, Hyde 1939, Robins 1971, Tate and Tate 1982.

Le Conte's Sparrow

Ammodramus leconteii



L 4¼"

RANGE: Breeds from east-central British Columbia, southern Mackenzie, and northern Saskatchewan to west-central Montana, northern North Dakota, and northern Michigan. Winters from west-central Kansas, southern Illinois, central Alabama, and South Carolina south to Texas, the Gulf Coast, and southeastern Georgia.

STATUS: Common.

HABITAT: Inhabits damp, grass-grown clearings, shallow prairie marshes, tall moist grasslands, sedge marshes often surrounded by bog and open fens in boreal forests. Prefers hummocky alkaline wetlands.

SPECIAL HABITAT REQUIREMENTS: Moist habitats with dense herbaceous vegetation.

NEST: Builds a well-concealed nest on or near the ground in the luxuriant growth of drier borders of open wetlands, usually of grasses interwoven among standing plant stems, generally in dense vegetation beneath tangles of old dead rushes, grasses, or sedges.

FOOD: Primarily eats insects during summer, but consumes mainly the seeds of weeds and grasses at other times. Gleans both insects and seeds from marsh plants. (Little is known about the food habits of this species.)

REFERENCES: Forbush and May 1955, Easterla 1962, Johnsgard 1979 Murray 1969, Walkinshaw in Bent 1968b.

Sharp-tailed Sparrow

Ammodramus caudacutus



RANGE: Breeds from east-central British Columbia, southern Mackenzie, and central Manitoba south to south-central Alberta, southeastern South Dakota, and northwestern Minnesota; also around James Bay, in southeastern Quebec, and along the Atlantic Coast from eastern Quebec south to North Carolina. Winters along the Atlantic Coast from New York south to Florida, the Gulf Coast west to Texas, and rarely in coastal California.

STATUS: Common along the coast, locally common inland.

HABITAT: In coastal areas, prefers short grasses in drier sections of salt or brackish marshes, especially where marshhay cordgrass and seashore saltgrass are present. Inland races inhabit freshwater marshes, marshy zones of prairie lakes and ponds, wet meadows, sloughs, and alkaline, hummocky fens.

SPECIAL HABITAT REQUIREMENTS: Well-drained sections of wetland with grassy or other herbaceous vegetation.

NEST: In coastal areas, builds nest in higher regions of marshes seldom flooded by tides, salt hay meadows, or the zone between marsh and upland. Elevates and conceals nest just above ground, sometimes attached to upright plant stems or placed in thick clumps of grass. Inland, nests are usually sunken in the ground but occasionally elevated.

FOOD: Forages on the banks of pools and creeks, gleaning primarily insects and small aquatic animals, but also seeds of grasses and weeds from the ground and low vegetation. Generally feeds throughout the marsh, although in coastal areas, prefers to forage in grass that is dense and matted.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Hill in Bent 1968b, Johnsgard 1979, Low and Mansell 1983, Murray 1969, Woolfenden 1956.

Seaside Sparrow

Ammodramus maritimus



L 5½"

RANGE: Breeds along the Atlantic Coast from Massachusetts south to northern Florida, and along the Gulf Coast from southern Texas east to western Florida. Winters throughout the breeding range to southern Florida, although most northern populations usually withdraw southward. Resident in southern and east-central Florida.

STATUS: Locally common, however the dusky race in east-central Florida is on the verge of extinction, and the Cape Sable race in southern Florida is endangered.

HABITAT: Inhabits short-grass tidal marshes and meadows (except for the Cape Sable race, which occurs in a narrow band of fresh and brackish marshes in southern Florida). Prefers rank stands of cordgrass along the borders of tidal creeks with muddy bottoms.

SPECIAL HABITAT REQUIREMENTS: Tidal salt marshes.

NEST: Builds nest above ground in cordgrass or rushes in wetter portions of salt marshes washed by the tide, on the ground in dense vegetation above the high tide mark, or in shrubs such as marsh-elders. Typically locates well-concealed nest up to a foot above ground. Generally, nests in wetter areas than the sharp-tailed sparrow.

FOOD: Eats mostly insects, crustaceans, and small marine life and some seeds of weeds and grasses. Prefers to forage in areas of open mud and smooth cordgrass along the edge of marshes, gleaning its prey from the ground and surrounding vegetation.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Petersen in Farrand 1983c, Sprunt in Bent 1968b, Stimson in Bent 1968b, Woolfenden 1956.

Fox Sparrow

Passerella iliaca

eastern race



western
race

L 6¼"

RANGE: Breeds from Alaska and the Yukon to northern Quebec and northern Labrador, south to northwestern Washington, in the western mountains to southern California and central Colorado, and east of the Rockies, across central Canada to southern Quebec. Winters from southern Alaska and southern British Columbia south through the Pacific States, and from central Arizona, Kansas and New Brunswick south to Mexico and central Florida.

STATUS: Common.

HABITAT: Fairly nonspecific in its requirements, needing only dense, shrubby undergrowth. Inhabits a wide variety of habitats throughout its range, including the undergrowth of deciduous or coniferous forests, brushy woodland edges, woodland thickets, chaparral, burns, cut over areas, scrub, riparian woodlands, willow thickets, and montane coniferous scrub.

SPECIAL HABITAT REQUIREMENTS: Dense shrubby undergrowth.

NEST: Commonly locates nest on the ground, well-concealed by surrounding tangles of vegetation, or in a bush or tree, typically less than 6 feet, but up to 20 feet above the ground. Prefers conifers for nesting.

FOOD: Feeds primarily on insects in summer and on seeds of weeds and some grasses in winter. Forages on the ground, scratching in leaf litter under shrubs and in weed patches.

REFERENCES: Austin in Bent 1968c, Forbush and May 1955, Terrill in Bent 1968c, Verner and Boss 1980.

Song Sparrow

Melospiza melodia



L 5½"

RANGE: Breeds from Alaska across Canada, south of Hudson Bay, to Newfoundland and south across the northern part of the United States, along the Pacific Coast, and into Mexico. Resident throughout the northern part of the United States and Pacific Coast. Winters coastally from Alaska and Newfoundland south throughout the southern half of the breeding range.

STATUS: Common throughout the eastern United States and northern parts of its range. Locally common in the West.

HABITAT: Inhabits moist areas with low irregular plants, or deep grassy and brushy vegetation. Particularly common along waterways, seacoasts with marshes of cattails or bulrushes, and along forest edges adjacent to bogs and openings. Also inhabits fencerows, thickets, hedgerows, and gardens.

SPECIAL HABITAT REQUIREMENTS: Moist areas with brushy vegetation.

NEST: Usually builds nest on the ground, concealed under a tuft of grass or bush, or even a brushpile, but sometimes in shrubs and small trees up to 12 feet above ground, and in tree cavities.

FOOD: Eats a wide variety of both vegetable and animal materials. Gleans insects from the ground, leaves, and branches, mostly during the breeding season.

REFERENCES: Nice 1937, 1943, Forbush and May 1955.

Lincoln's Sparrow

Melospiza lincolnii



L 4 3/4"

RANGE: Breeds from western central Alaska across most of Canada, south along the Pacific Coast and the Rocky Mountains in southern California and northern New Mexico, and into the northern Lake States and northern New England. Winters from southern California, southern Arizona, Texas, and New Mexico south throughout Mexico to Costa Rica. Migrates throughout continental North America between its breeding and wintering ranges.

STATUS: Common.

HABITAT: Prefers bogs, wet meadows, and riparian thickets. Also inhabits hedgerows, fencerows, and the understory of open woodlands, as well as forest edges, clearings, and shrubby areas.

SPECIAL HABITAT REQUIREMENTS: Thickets along the edge of fields, waterways, or in wet meadows.

NEST: Usually places nest on the ground in a shallow depression. Builds a rather frail structure of leaves, moss, and some grasses.

FOOD: Eats both animal and vegetable materials. During breeding season, mostly eats animal material, including a variety of insects, spiders, and millipedes. During winter, mostly eats grain and grass seed.

REFERENCES: Forbush and May 1955.

Swamp Sparrow

Melospiza georgiana



L 5"

RANGE: Breeds from west-central and southern Mackenzie and northern Manitoba across to southern Labrador, and south to northeastern and east-central British Columbia, the Dakotas, northern Illinois, and Maryland. Winters from eastern Nebraska through the Great Lakes region to Massachusetts, south to Texas, the Gulf Coast, and Florida, and west across New Mexico to southeastern Arizona.

STATUS: Common.

HABITAT: Wetlands with bushes, rank marsh grasses, sedges, and reeds are characteristic habitat. Inhabits brushy wet meadows, sloughs, bogs, swamps, freshwater marshes, along swampy shorelines of lakes or streams, and rarely in coastal brackish meadows. Avoids heavily wooded wetlands. In winter, frequents springs, seeps, and open brooks that have brushy cover nearby.

SPECIAL HABITAT REQUIREMENTS: Swampy wetlands with rank emergent vegetation.

NEST: Often builds nest among cattail stalks, upon clumps of bent over vegetation, on sedge tussocks, or in bushes, frequently directly over water that may be 2 feet or more deep. Usually places nest about 12 inches above ground or water, preferably in areas with mixed vegetation rather than in pure cattails.

FOOD: Feeds mainly on insects in spring and early summer, and on the seeds of marsh plants in late summer and fall. Gleans food while wading in shallow water or from surrounding vegetation.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Low and Mansell 1983, Martin et al. 1951, Petersen in Farrand 1983, Wetherbee in Bent 1968c.

White-throated Sparrow

Zonotrichia albicollis



RANGE: Breeds from southeastern Yukon and west-central and southern Mackenzie to southern Labrador and Newfoundland south to central interior British Columbia, north-central North Dakota, northern Wisconsin, and northern New Jersey. Winters from southeastern Iowa and southern Wisconsin east to Massachusetts, south to Mexico, the Gulf Coast, and Florida, and west across Texas to California.

STATUS: Abundant.

HABITAT: Inhabits coniferous and northern deciduous forests, favoring semiopen wooded areas with dense undergrowth or brush, including brushy clearings, cutover woodlands, second-growth, forest edges, borders of swamps and bogs, and other shrubby growth. Seldom found far from dense cover.

SPECIAL HABITAT REQUIREMENTS: Open woodlands with dense cover in the form of dense woody undergrowth, thickets, or brush.

NEST: Usually builds nest on the ground at the edge of a clearing in areas with small trees, clumps of shrubs, and extensive ground cover of herbs, grasses, and often blueberries. Usually locates nest near a large object such as a tree, stump, or log that possibly serves as a lookout perch; conceals nest by surrounding ground vegetation. Occasionally nests above ground in dense bushes, roots of upturned stumps, or in brush heaps.

FOOD: Feeds primarily on the seeds of grasses and weeds, and on wild fruits, but consumes a considerable quantity of insects when available. Forages largely on the ground, scratching in leaf litter or gleaning weeds and grasses for its food.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Lowther and Falls in Bent 1968c.

Golden-crowned Sparrow

Zonotrichia atricapilla



RANGE: Breeds from western and north-central Alaska along the coastal region, south-central Yukon, southern British Columbia, and into the extreme northern part of Washington. Winters from southern Alaska and southern British Columbia, mostly west of the Cascades, to northern Baja California. Also occurs in southeastern California and parts of Arizona, Utah, Colorado, and New Mexico.

STATUS: Common.

HABITAT: Generally inhabits high-elevation thickets and shrubs, and often dwarf conifers found in brushy canyons. In winter, found in dense brush thickets and chaparral, and gardens along the West Coast.

SPECIAL HABITAT REQUIREMENTS: Openings in high-elevation coniferous forests, particularly spruce forests.

NEST: Builds a nest of bulky material, such as ferns, leaves, and dry grass, on the ground or above ground on horizontal branches of small trees, usually well concealed.

FOOD: Eats mainly seeds, shoots from plants, buds, and flowers of grasses and forbs. Also gleans small insects from trees, branches, shrubs, and grass.

REFERENCES: Verner and Boss 1980.

White-crowned Sparrow

Zonotrichia leucophrys



RANGE: Breeds throughout Alaska, the northern regions of Canada surrounding the Arctic Ocean-Hudson Bay region, east to the Atlantic, south through the Yukon and British Columbia, through the Rocky Mountains, west to the Pacific Coast and the Sierra Nevadas. Winters throughout most of the United States, except Florida and the northern Great Plains, and in Mexico.

STATUS: Abundant.

HABITAT: Frequents valleys, brushy hillsides, roadside vegetation, and cultivated fields. In arctic regions, inhabits open stunted tree growth and brushlands. Uses edge habitats and brush piles during winter.

SPECIAL HABITAT REQUIREMENTS: Thickets, hedgerows, or edge.

NEST: Often builds nest consisting of grassy materials, mosses, and lichens, lined with rootlets or animal hairs, placing it on the ground in a moss or lichen bed, in grassy areas, but sometimes on the lower branches of shrubbery. Most nests are well concealed and difficult to locate.

FOOD: Obtains both plant and animal foods by scratching in the soil. Eats the fruiting bodies of mosses, as well as a variety of seeds, and capitalizes on outbreaks of insects.

REFERENCES: Beal and McAtee 1912, Forbush and May 1955.

Harris' Sparrow

Zonotrichia querula



RANGE: Breeds from northwestern and east-central Mackenzie and southern Keewatin south to northeastern Saskatchewan and northern Manitoba. Winters primarily along the eastern edge of the Great Plains, although it may be found from southeastern Alaska and southern British Columbia to northern Colorado and central Iowa, and south to California, Texas, and western Tennessee.

STATUS: Fairly common.

HABITAT: Breeds in the Canadian subarctic, in open clearings, woodland edges, and brushy margins of burned-over areas bordered by spruce forests. During winter, inhabits brushy habitats, preferring woodlot borders and hedgerows.

NEST: Builds nest in the ground, usually in mossy hummocks surrounded by water near stunted spruce trees, often under a low shrub on a sheltered southern exposure. May also locate nest in dry clearings under small trees within 100 feet of a lake.

FOOD: At all seasons, chiefly eats seeds of weeds, grasses, and wild fruits, but includes insects in diet, especially in summer. Primarily feeds on the ground.

REFERENCES: Baumgartner in Bent 1968c, Forbush and May 1955, Kaufman in Farrand 1983c, Semple and Sutton 1932.

Dark-eyed Junco

Junco hyemalis



Oregon race

L 5¼"



Slate-colored
race



Gray-headed race.

RANGE: Breeds from Alaska and central Yukon to Labrador and Newfoundland, south to central coastal California, in the mountains to eastern California, central Arizona, and western Texas, southern Alberta, northern and east-central Minnesota, central Michigan, southern New England, and in the Appalachian Mountains to northern Georgia and northwestern South Carolina; also in the Black Hills. Winters from central and south coastal Alaska, coastal British Columbia and across southern Canada south to Mexico, the Gulf Coast, and northern Florida.

STATUS: Common to abundant.

HABITAT: Occurs from sea level to timberline in a variety of wooded habitats that have openings with dense herbaceous ground cover, including coniferous and deciduous forests, forest edges, woodland clearings, stream borders, open woodlands, brushy cover bordering mountain meadows, and old burns. Avoids deep forest interiors in favor of woodland edges and openings. In winter, prefers weedy fields but also inhabits open woodlands, hedgerows, suburbs, and farmyards.

SPECIAL HABITAT REQUIREMENTS: Openings in wooded habitats covered with dense herbaceous vegetation such as grasses or forbs.

NEST: Commonly builds nest on the ground near the edge of openings in wooded areas or in a slight depression, usually well concealed under weeds, grasses, fallen logs, tree roots, or other overhead shelter. Occasionally may place nest up to 8 feet above ground in a shrub or tree.

FOOD: Forages on the ground, picking up seeds (mostly) and insects.

REFERENCES: Barrowclogh in Farrand 1983c, Beal and McAtee 1912, DeGraff et al. 1980, Eaton in Bent 1968b, Hostetter 1961, Martin et al. 1951, Phelps in Bent 1968b, Sprunt in Bent 1968b, Thatcher in Bent 1968b, Whitney in Bent 1968b.

Yellow-eyed Junco

Junco phaeonotus



L 5½"

RANGE: Resident from southern Arizona and parts of New Mexico to central Mexico.

STATUS: Locally common.

HABITAT: Prefers coniferous forests and pines or oaks that are relatively open, usually above 5,000 feet. Often inhabits areas adjacent to scrub, pastures, and fields.

SPECIAL HABITAT REQUIREMENTS: Coniferous and pine-oak forests; edge-type habitat appears to be important.

NEST: Usually builds cup-shaped nest on the ground under a clump of grass or log, near a flat stone, or sometimes on the ground under a drooping pine limb or in a thick shrub.

FOOD: Feeds primarily on seeds and other vegetable material as well as some insects. Forages on the ground, but occasionally removes animal or vegetable material from the limbs of trees. Occasionally eats fruits.

REFERENCES: Bent 1968b.

McCown's Longspur

Calcarius mccownii



RANGE: Breeds from southeastern Alberta east to north-central North Dakota, and south to northeastern Colorado and northwestern Nebraska. Winters from central Arizona, west-central Kansas, and central Oklahoma south into Mexico.

STATUS: Uncommon.

HABITAT: Inhabits dry shortgrass prairie, plowed and stubble fields, grazed pastures, dry lake beds, and other sparse, bare, dry grounds on the western plains.

SPECIAL HABITAT REQUIREMENTS: Open, dry, sparsely vegetated prairie.

NEST: Places nest in a shallow depression on the ground, sometimes in a clump of grass or under a shrub, but usually amid sparse prairie vegetation. Typically builds a nest that is open above, covered only by a few blades of grass, although occasionally it may be concealed by overhanging shrub branches. Rarely, places nest above ground in a shrub.

FOOD: Forages on the ground, picking up seeds of weeds and grasses, and insects, especially grasshoppers.

REFERENCES: DuBois 1937, Johnsgard 1979, Kaufman in Farrand 1983c, Kraus in Bent 1968c, Mickey 1943.

Lapland Longspur

Calcarius lapponicus



RANGE: Breeds from western and northern Alaska and northern Yukon across northern Canada, including many islands to Labrador, and south to south-coastal Alaska and southern Keewatin. Winters from coastal southern Alaska and southern British Columbia across the northern United States to Nova Scotia, and south to southeastern California, Colorado, Arkansas, and Maryland; casually farther south.

STATUS: Abundant on breeding grounds; local in interior.

HABITAT: Breeds in arctic and subarctic tundra, preferring areas of wide, moist tundra covered with grassy tussocks or hummocks and interspersed with ponds and streams. Inhabits moist sedge meadows, swampy flats, marshes, and moist grasslands, preferring sedge tussocks or ridges covered with low willows, or dwarf birch intermixed with heath. Avoids extremely wet areas unless elevated sites are available. In winter, found in stubble fields, barren grounds, beaches, prairies, or open weedy meadows.

SPECIAL HABITAT REQUIREMENTS: Moist tundra on relatively level terrain with elevated sites such as tussocks, hummocks, or low ridges, and concealing vegetation.

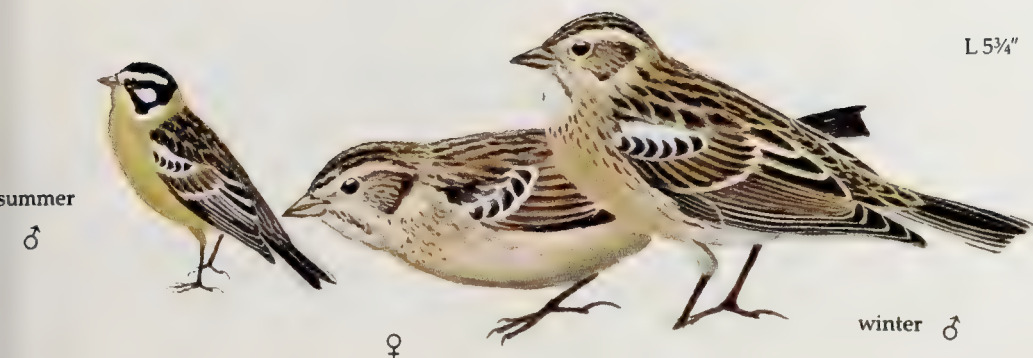
NEST: Usually places nest in a depression in the side of a small hummock or tussock, protected by overhanging grass, sedge, or leafy twigs of shrubs. Uses drier, elevated sites for nesting rather than low, wet, surrounding terrain.

FOOD: In summer, eats mostly insects and the seeds of a variety of plants; in winter, feeds mainly on seeds of weeds and grasses. Gleans food from the ground.

REFERENCES: DeGraff et al. 1980, Jehl 1968, Williamson in Bent 1968c.

Smith's Longspur

Calcarius pictus



RANGE: Breeds in east-central Alaska and adjacent British Columbia, and from northern Alaska east across northern Canada to extreme northern Ontario. Migrates through the northern Great Plains. Winters from Kansas and Iowa south to Oklahoma, Texas, and Louisiana.

STATUS: Uncommon.

HABITAT: Inhabits dry, grassy, hummock areas in tundra, often where there are dry sedge meadows dominated by dwarf birch and scattered black spruce. Prefers areas with a perch site, often using small spruces. Winters in grassy and weedy fields, prairies, and along edges of open areas such as airport runways and roadways.

SPECIAL HABITAT REQUIREMENTS: Small isolated trees in tundra areas for perches.

NEST: Builds a nest, commonly unprotected from above, in a small depression in a relatively dry, flat hummock, usually on a hummock ridge or at the base of a small tree or shrub.

FOOD: Eats a variety of foods during summer; largely plant material, principally seeds (90 percent in the first part of June.) Also eats invertebrates when available, including ants, spiders, and beetles. Commonly eats immature insects in the latter part of the summer.

REFERENCES: Jehl 1968.

Chestnut-collared Longspur

Calcarius ornatus



RANGE: Breeds from southern Alberta, Saskatchewan, and Manitoba, east of the Rockies to northeastern Colorado and western Kansas. Winters from northern Arizona, central and northern New Mexico, eastern Colorado, and central Kansas south into Mexico. Occurs rarely in California.

STATUS: Common.

HABITAT: Inhabits shortgrass plains and prairies (cultivation has reduced breeding habitat.) In winter, tends to congregate on cultivated fields, and along edge areas, fencerows, and roadways.

SPECIAL HABITAT REQUIREMENTS: Shortgrass prairie.

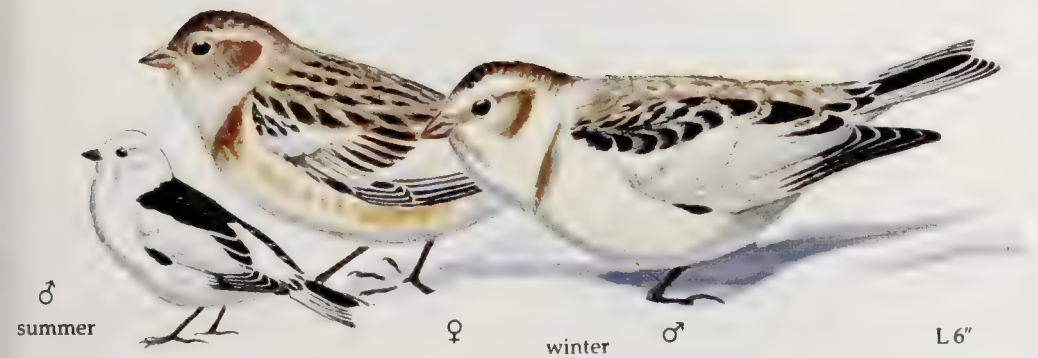
NEST: Builds nest on the ground, usually in a small depression in grass in uncultivated grassland with occasional low ridges and shallow areas. Seems to prefer nest sites in moist areas. In flooded meadows, places nest on an elevated site.

FOOD: Feeds primarily on grass seed and some insects, which are gleaned from the ground. During winter, feeds almost entirely on plant material.

REFERENCES: Forbush and May 1955.

Snow Bunting

Plectrophenax nivalis



RANGE: Breeds in Arctic tundra from northern Alaska to Prince Patrick and northern Ellesmere islands, south to extreme northwestern British Columbia, east-central Mackenzie, central and southeastern Keewatin, and northern Labrador. Winters from west-central and southern Alaska and southern Canada south to California, Colorado, Missouri, and North Carolina, casually farther south.

STATUS: Common.

HABITAT: Breeds in rough, rocky Arctic tundra with scattered vegetation. Prefers stony beaches, rocky escarpments, and cliffs, occurring less commonly in grassy tundra. In winter, inhabits open country, along lake shores, beaches, and roadsides, and grassy, weedy, or stubble fields.

SPECIAL HABITAT REQUIREMENTS: Rocky areas with sparse vegetation.

NEST: Nearly always places nest in a hole or cranny, in a variety of natural and artificial sites, often a foot or more back in narrow rock crevices under loose rocks on the ground. May place nest in a depression or in cracks in the ground if other sites are lacking but rarely exposed on open ground.

FOOD: In winter, primarily eats seeds of weeds and grasses gleaned from the tips of plants and the surface of the snow. Adds insects and spiders to the diet during summer.

REFERENCES: DeGraff et al. 1980. Forbush and May 1955, Parmelee in Bent 1968c, Sutton and Parmelee 1954b.

Bobolink

Dolichonyx oryzivorus



RANGE: Breeds from southern interior British Columbia across southern Canada and central Ontario south to eastern Oregon, central Colorado, central Illinois, and central New Jersey. Winters in South America.

STATUS: Locally common, although numbers are decreasing in the Northeast due to a decline in agriculture; extending range in the West because of irrigation.

HABITAT: Prefers large open fields of tall grass, alfalfa, clover, or grain crops, but also inhabits wet meadows, ungrazed to lightly grazed mixed-grass prairies, and fallow fields. During migration, frequents marshes and grain fields.

SPECIAL HABITAT REQUIREMENTS: Large expanses of grassland or forb cover.

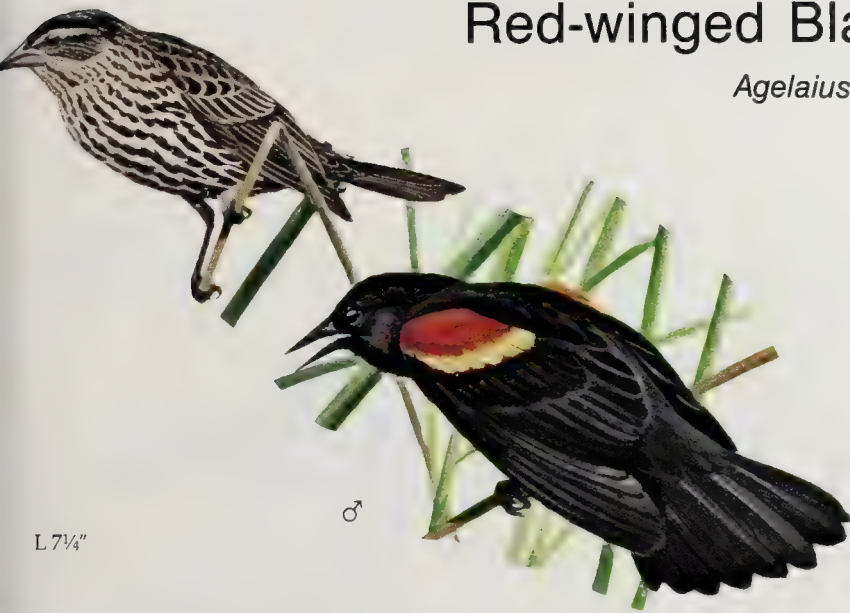
NEST: Builds nest on the ground, usually in a hollow scraped in the ground or in a natural depression, rarely above ground attached to plant stems. Always locates nest in dense stands of tall vegetation such as hay, alfalfa, clover, or thick growths of weeds.

FOOD: Prefers to forage in cultivated grain fields, gleaning insects, seeds of weeds and grasses, and waste grain from standing vegetation and on the ground.

REFERENCES: Beal 1900, Bent 1958, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979.

Red-winged Blackbird

Agelaius phoeniceus



L 7¼"

RANGE: Breeds from the southern tip of Alaska, and Yukon down to northern Washington, across the northern part of the United States and Canada including Idaho, Montana, Wyoming, the Great Lakes, and New England. Resident in the rest of the United States south into Baja California, Mexico, and Central America. Northern birds migrate southward in winter.

STATUS: Abundant.

HABITAT: Breeds in marshes and agricultural areas, usually where there are wetlands and also along the edge of hayfields, old fields, and pastures. Prefers areas with trees nearby and where habitat edges are abundant; often perches on old erect vegetation. Is extremely territorial, partitioning territories into areas of several hundred square feet, thus efficiently limiting the numbers that can exploit a resource. Flocks in the winter and moves throughout fields and marshy areas.

SPECIAL HABITAT REQUIREMENTS: Standing vegetation along open fields and marshes.

NEST: Nests in a deep narrow cup of grass, reeds, and weed rootlets, usually attached to emergent vegetation (particularly cattails) up to 12 feet above ground. Also nests in weeds and brush patches, croplands such as alfalfa and cereal grains, even upland areas of mixed chaparral.

FOOD: Consumes a diet consisting of both vegetable and animal material, including a variety of grains and seeds, insects, spiders, mites, and snails. Often descends in large numbers on cultivated fields, eating a great deal of the grain.

REFERENCES: Albers 1978, Beal 1900, Case and Hewitt 1963, Lowe and Mansell 1983, Mott et al. 1972, Orians 1961, Payne 1969.

Tricolored Blackbird

Agelaius tricolor



RANGE: Breeds from southern Oregon east of the coast range south through interior California along the Pacific Coast from central California to northwest Baja California. Resident from northern California south throughout breeding range and adjacent agricultural areas. Some northern birds are migratory.

STATUS: Common.

HABITAT: Commonly breeds in freshwater marshes of cattail, tule, bulrush, and sage. Roosts in the strips along marshes between rice fields. Feeds and roosts in dense flocks, ranging from 4 to over 20,000 in a colony, throughout the year. In winter, moves through marshes, open cultivated lands, and pastures.

SPECIAL HABITAT REQUIREMENTS: Cattail or tule marshes.

NEST: Builds nest of cattails, sedges, grasses, or other aquatic vegetation gathered from the surface or in shallow water, and attached to cattails or twigs in shrubs and blackberry thickets, usually near water. Prefers live emergent vegetation for nesting.

FOOD: Gleans food from the ground and low vegetation; eats insects, spiders, and occasionally small tadpoles and snails. In winter, eats rice and a variety of grain crops.

REFERENCES: Payne 1969.

Eastern Meadowlark

Sturnella magna



L 8½"

RANGE: Breeds from northern Minnesota and southern Ontario across to southern New Brunswick, south through the Eastern United States to Texas, the Gulf Coast, Central America, and Florida, and west to southwestern South Dakota, central Nebraska and central Arizona. Winters from central Arizona, Kansas, central Wisconsin, New England, and Nova Scotia south throughout the breeding range, although casually farther north.

STATUS: Common, although there are widespread declines in the Eastern States.

HABITAT: Prefers pastures, but also occurs in other grass-dominated habitats such as hayfields, grassy meadows, tallgrass prairies, open fields of corn, alfalfa, and clover, and weedy orchards. Prefers moist meadows and lowlands at the western edge of its range, where distribution overlaps that of the western meadowlark.

SPECIAL HABITAT REQUIREMENTS: Open grasslands with elevated singing perches such as fences, poles, or lone trees.

NEST: Builds nest on the ground in a natural depression or scrape, well concealed by a canopy of vegetation bent over the nest, preferably in cover 10 to 20 inches high.

FOOD: Gleans food from the ground and low vegetation. During summer, mainly eats insects; in winter, primarily eats seeds of weeds and grasses, and waste grain, except in southerly states where insects are still available.

REFERENCES: Bent 1958, Johnsgard 1979, Lanyon 1957, Roseberry and Klimstra 1970, Tate and Tate 1982.

Western Meadowlark

Sturnella neglecta



L 8½"

RANGE: Breeds from central British Columbia, north-central Alberta, Saskatchewan, and central Canada, south throughout most of the Western United States. Found in most areas west of the Mississippi. Resident throughout the Pacific, southern Rocky Mountain, and southern Great Plain States. Winters also in Oklahoma, Texas, and along the coasts of Mexico and Baja California.

STATUS: Common.

HABITAT: Typically inhabits grasslands, savannahs, cultivated fields, and pastures, preferring open fields with perch sites such as fences, old logs, or dead trees.

SPECIAL HABITAT REQUIREMENTS: Open grasslands.

NEST: Builds nest in a shallow depression on dry ground in open grassland, often in grass or a small grass tuft, sometimes in rocky areas. Usually uses grasses for nest material.

FOOD: Gleans food from the ground or low vegetation. Eats both animal and vegetable material; about 70 percent animal material, mainly beetles, but also a variety of other insects and invertebrates; and a variety of grains and seeds.

REFERENCES: Lanyon 1957.

Yellow-headed Blackbird

Xanthocephalus xanthocephalus



L 8½"

RANGE: Breeds from southern and central Canada, throughout the western part of the United States, west of the Mississippi River. Winters from southern California, Arizona, New Mexico, and Texas into Mexico.

STATUS: Common.

HABITAT: Inhabits freshwater marshes of cattails, bulrushes, and reeds, generally over water. Winters in open cultivated fields, pastures, and marshes.

SPECIAL HABITAT REQUIREMENTS: Marshy vegetation.

NEST: Generally nests in colonies. Builds a woven basketlike cup nest of marsh vegetation lined with fine grass and attaches it to reeds and cattails 1 to 3 feet above water or sometimes in willows in wet areas.

FOOD: Eats both vegetable and animal material gleaned from the ground, mostly vegetative material, which includes seeds and leaves of grasses and forbs, and grain crops.

REFERENCES: Beal 1900, Forbush and May 1955, Lowe and Mansell 1983, Willson 1966.

Rusty Blackbird

Euphagus carolinus



RANGE: Breeds from western and north-central Alaska and northern Yukon to southern Keewatin, northern Quebec and central Labrador south to southwestern and south-coastal Alaska, central interior British Columbia, central Manitoba, northern New England, and northeastern New York. Winters from south-coastal Alaska and southeastern British Columbia to southern Ontario and southern New England south to Texas, the Gulf Coast, and northern Florida, and west to central Colorado.

STATUS: Fairly common.

HABITAT: Almost always found near water, breeding in boggy spruce woods, along swampy wooded shores of lakes, streams, tree-bordered marshes, beaver ponds, and swamps; and on wooded islands in lakes. Rarely occurs in fields with other blackbirds. In winter, does not stay so close to water, occurring also in open woodland, scrub, pastures, weedy gardens, and cultivated land.

SPECIAL HABITAT REQUIREMENTS: Wooded wetlands during the breeding season.

NEST: Nests in dense growths of evergreens, especially second-growth spruce or balsam, 2 to 20 feet, but typically less than 10 feet above the ground. Also uses dead trees or clumps of deciduous bushes such as buttonbush or sweetgale along streamsides for nesting.

FOOD: Forages by gleaning insects, weed seeds, waste grain, and wild fruit from the ground in pastures, fields, or grassy edges of wetlands, or by wading in shallow water.

REFERENCES: Beal 1900, Bent 1958, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Kaufman in Farrand 1983c, Kennard 1920.

Brewer's Blackbird

Euphagus cyanocephalus



RANGE: Breeds from southwestern and central British Columbia to southern Ontario, south throughout the northern United States; resident in the Pacific Coast, Great Plains, and Rocky Mountain states. Winters from southern British Columbia, east-central Montana, and the northern portions of the Gulf States, south to Baja California, northern Mexico, southern Texas, the Gulf Coast, and Florida.

STATUS: Common.

HABITAT: Prefers to be near water in habitats such as riparian woodlands, aspen groves, parklands, cultivated lands, and marshes; often found around human habitation. Uses bulrushes and pines for roosting and daytime resting places and displays from the tops of pine trees. In winter, frequents pastures and fields.

SPECIAL HABITAT REQUIREMENTS: Marshlike areas.

NEST: Nests singly or in loose colonies on the ground or in trees and shrubs 20 to 30 feet above the ground. Places the cup-shaped nest usually at or near the end of a branch.

FOOD: Consumes a diet of about 68 percent vegetative and 32 percent animal material gleaned mostly from the ground. Commonly follows plows searching for insects.

REFERENCES: Beal 1900, Terres 1980, Williams 1952.

Great-tailed Grackle

Quiscalus mexicanus

RANGE: Resident from southern California, southern Nevada, southeastern Colorado, Kansas, and southwestern Missouri south through Mexico to South America.

STATUS: Common.

HABITAT: Inhabits a variety of climatic regions and uses a diversity of plant types for nesting. Basically needs standing water and open ground for foraging; does not occur in forests or at great distances from water. In deserts and prairie country, only occurs near water courses or irrigated agricultural areas where trees are available.

SPECIAL HABITAT REQUIREMENTS: Partially open situations with scattered trees and water.

NEST: Nests colonially; builds a bulky cup nest of grass, sticks, and seaweed or Spanish moss that is lined with grass and rootlets. Locates nest 2 to 60 feet above ground in a variety of tree species or may build it in reeds over water when trees are unavailable.

FOOD: Gleans its food from the ground, occasionally wading in shallow water. Eats grains, berries, mollusks, crustaceans, insects, small fish, young birds, and eggs.

REFERENCES: Lowe and Mansell 1983, Pruitt 1975, Selander and Giller 1961.

Boat-tailed Grackle

Quiscalus major



BOAT-TAILED
GRACKLE
L 16"

GREAT-TAILED
GRACKLE
L 12-16"

RANGE: Resident along the Atlantic Coast from New York to Florida, and west along the Gulf Coast to Texas.

STATUS: Common.

HABITAT: Prefers open coastal marshes near large bodies of brackish or salt water, but also inhabits large tidal rivers short distances inland, city parks, and farmland. In Florida, inhabits inland freshwater habitats on the peninsula as well as coastal marshes. Seldom occurs more than a few miles inland.

SPECIAL HABITAT REQUIREMENTS: Coastal fresh or saltwater wetlands.

NEST: Nests in colonies in cattails, bulrushes, marsh-grass, bushes, or trees, from 6 inches to 80 feet above the ground. Usually builds nest in vegetation growing in water or in branches hanging over water. Prefers to nest in marsh vegetation, often selecting marsh habitat over trees near water.

FOOD: Finds most of its food on the ground by probing in mud and litter or turning over shells or stones. Commonly forages in marshy areas, mudflats, and the margins of ponds, lakes, and streams. Eats insects, fish, frogs, crayfish, mollusks, young birds and eggs, rice, waste grains, and berries.

REFERENCES: Beal 1900, Low and Mansell 1983, McIlhenny 1937, Pruitt 1975, Selander and Giller 1961, Tutor 1962.

Common Grackle

Quiscalus quiscula



L 10-12"

RANGE: Breeds from northeastern British Columbia and southern Mackenzie to southwestern Newfoundland, south to central and southeastern Texas, the Gulf Coast and southern Florida, and west to eastern Wyoming, central Colorado, and central and southeastern New Mexico. Winters from Kansas, Iowa, the southern Great Lakes region, New England, and Nova Scotia south to southeastern New Mexico, southern Texas, the Gulf Coast, and Florida.

STATUS: Abundant.

HABITAT: Prefers open habitat (especially agricultural) with scattered trees or open woodlands, forest edge, and nearby human habitation. Frequents city parks, swamps, brushy or reedy marshes, and cultivated lands, especially in migration.

NEST: Builds nest in a variety of trees and often has local preferences for tree species. Nests colonially, building nests 7 to 35 feet above the ground (average 20 feet); most are well concealed in dense masses of foliage.

FOOD: Forages for food in cultivated fields, shrubs, and shallow water. Eats nuts, weed seeds, small bulbs, eggs and young of other birds, and fish; can be a pest when large numbers descend on cultivated crops.

REFERENCES: Beal 1900, Forbush and May 1955, Jones 1969, Maxwell 1970.

Bronzed Cowbird

Molothrus aeneus



RANGE: Resident from extreme southeastern California, southern Arizona, New Mexico, and Texas south through central Mexico to Panama.

STATUS: Locally common.

HABITAT: Inhabits mostly open country with occasional tree patches or large tall shrubs. Prefers humid, hot climate, often in areas where cattle are grazed and is common in areas of human habitation.

SPECIAL HABITAT REQUIREMENTS: Open areas with scattered trees or shrubs.

NEST: Builds no nest; generally lays its eggs in the nests of other birds, preferably those nesting in brush, semi-open to open ranch, farm, and residential areas.

FOOD: Eats weed and grass seeds, grain, and insects that are gleaned from the ground. Also eats insects from the skin of livestock. Commonly feeds and roosts in large flocks.

REFERENCES: Oberholser 1974b.

Brown-headed Cowbird

Molothrus ater



RANGE: Breeds from southeastern Alaska, northern British Columbia, and southern Mackenzie east to southern Quebec and southern Newfoundland, and south to Mexico, the Gulf Coast, and central Florida. Winters from northern California, central Arizona, the Great Lakes region, and New England south to Mexico, the Gulf Coast, and southern Florida.

STATUS: Common.

HABITAT: Prefers habitats where low or scattered trees are interspersed with grassland vegetation. Originally occupied open grasslands and avoided unbroken forestlands, but due to agriculture, cattle grazing, and deforestation, occupies a much expanded range. Now found in open coniferous and deciduous woodlands, forest edges, brushy thickets, agricultural land, and suburban areas.

SPECIAL HABITAT REQUIREMENTS: Habitats with open grassy spaces.

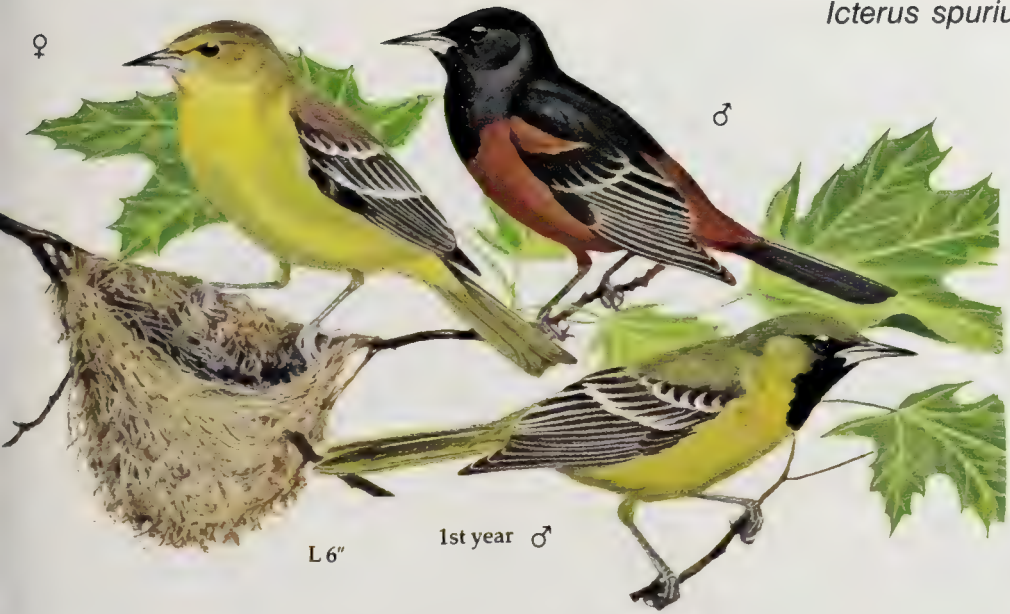
NEST: Builds no nest; lays its eggs in the nests of over 100 species of birds, particularly tyrant flycatchers, finches, vireos, and warblers.

FOOD: Gleans weed seeds, which form over half of the diet, as well as grass seeds, waste grain, and insects from the ground. Commonly forages in pastures searching for insects stirred up by cattle.

REFERENCES: Beal 1900, Bent 1958, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Mayfield 1965.

Orchard Oriole

Icterus spurius



RANGE: Breeds from southeastern Saskatchewan, southern Manitoba, and central Minnesota east to northern Massachusetts, south to Mexico, Texas, the Gulf Coast and central Florida, and west to eastern Colorado. Winters from Mexico to South America, casually to southern Texas, rarely in coastal California.

STATUS: Locally common, but populations are decreasing from Kansas to Alabama.

HABITAT: Prefers orchards and open country with a few scattered trees. Also breeds in residential areas, farmlands, shelterbelts, woodland margins, and lightly wooded river bottoms. At times, it may inhabit marshes and bordering trees. Heavily wooded or dense forests are avoided.

SPECIAL HABITAT REQUIREMENTS: Open woodlands or open areas with scattered trees.

NEST: Suspends semipendulous nest, well concealed by dense foliage, from a fork or crotch of a variety of trees and shrubs 4 to 70 feet, typically 10 to 20 feet, above the ground. Commonly nests in trees also supporting Eastern kingbird nests.

FOOD: Gleans insects, which form over 90 percent of the diet, from leaves of trees and shrubs. Also eats fruits.

REFERENCES: Bent 1958, DeGraff et al. 1980, Dennis 1948, Forbush and May 1955, Johnsgard 1979, Tate and Tate 1982.

Hooded Oriole

Icterus cucullatus



RANGE: Breeds from northern coastal and central California, southern Nevada, central Arizona, and western Texas south into northern Mexico. Resident in southern Baja California and throughout mainland Mexico.

STATUS: Common.

HABITAT: Inhabits palm trees, mesquite, dry shrubs, and some deciduous and riparian woodlands; often found around ranches and towns.

NEST: Usually constructs a large, hanging nest with a variety of grasses, Spanish moss, thin branches, as well as dry vegetables, hair, and other local materials woven together, and suspends it from the limbs of trees or cacti.

FOOD: Eats a variety of insects, along with flower nectar, fruit, and other plant materials.

REFERENCES: Phillips et al. 1964, Terres 1980.

Altamira Oriole

Icterus gularis



L 8½"

RANGE: Resident from the lower Rio Grande Valley in extreme southern Texas south through Mexico to Central America.

STATUS: Rare.

HABITAT: Inhabits open woodlands, trees along fields and streams, scattered groves in pastures, and hillsides.

NEST: Fastens conspicuous pensile pouch nest, 1 to 2 feet long, to the ends of slender, strong, flexible terminal twigs, 12 to 35 feet above the ground. Usually places nest in ebony blackbead, mesquite, or willow.

FOOD: Forages among the leaves of trees for insects and fruits; also eats caterpillars, spiders, small figs, and berries.

REFERENCES: Bent 1958, Oberholser 1974b, Sutton and Pettingill 1943, Terres 1980.

Audubon's Oriole

Icterus graduacauda



RANGE: Resident in southern Texas and Mexico.

STATUS: Uncommon.

HABITAT: Inhabits dense forests along stagnant water courses or old stream beds, occurring in mesquite, hackberry, ebony blackbead, or huisache with a thick undergrowth of shrubs or small trees. Also frequents thickets in forest openings.

NEST: Attaches half-pensile nest to upright terminal branches, twigs, and leaves 6 to 14 feet above the ground. Places nest in dense cover, usually mesquite.

FOOD: Forages at midlevel in trees in dense woods for insects and small fruits.

REFERENCES: Bent 1958, Kaufman in Farrand 1983c, Oberholser 1974b.

Northern Oriole

Icterus galbula



RANGE: Breeds from southern interior British Columbia and central Alberta to central Maine and central Nova Scotia, south to southern Texas, Mexico, the central Gulf States, central North Carolina, and Delaware. Winters along the Gulf Coast and from Mexico to South America.

STATUS: Common.

HABITAT: In the East, inhabits orchards, deciduous forest edges, wooded river bottoms, upland forests, partially wooded suburban areas, parks, and shelterbelts. In the west, prefers semiarid mesquite groves and deciduous trees bordering streams or irrigation ditches in open country, prairie, or cultivated areas.

SPECIAL HABITAT REQUIREMENTS: Tall deciduous trees for nesting.

NEST: Usually attaches pendant nest by its rim to the tip of a long drooping branch, 9 to 70 feet, but typically 25 to 30 feet above the ground. Most frequently uses large trees, especially elms and cottonwoods growing in the open, but will use a wide variety of deciduous trees throughout its range.

FOOD: Primarily gleans insects from leaf and twig surfaces; also eats a few spiders and some wild and cultivated fruit.

REFERENCES: Bent 1958, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Typer in Bent 1958.

Scott's Oriole

Icterus parisorum



RANGE: Breeds from southern California, Nevada, Utah, western Colorado, central New Mexico, and western Texas south into Mexico. Winters from southern California to southern Mexico.

STATUS: Common.

HABITAT: Prefers pinyon-juniper woodlands of montane semidesert areas, live oak-yucca associations, and sycamores and cottonwoods in canyons. Also uses joshua-tree habitat.

SPECIAL HABITAT REQUIREMENTS: Yucca, pinyon-juniper, or oak trees in arid areas.

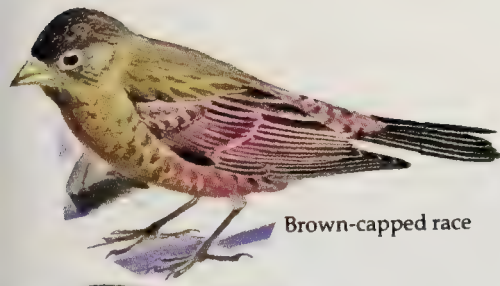
NEST: Constructs a cup-shaped nest with fibers of local grasses, weeds, and other vegetative material and suspends it from branches of almost any available tree, including joshua-trees and yucca plants.

FOOD: Probes flowers for nectar and small insects; also eats other insects, berries, and cactus fruits.

REFERENCES: Phillips et al. 1964, Terres 1980.

Rosy Finch

Leucosticte arctoa



Brown-capped race

♂



Black race



Gray-crowned race

L 6"

RANGE: Breeds above timberline from Alaska to southwestern Alberta and south through the Cascades, Sierra Nevada, and the Rocky Mountains to east-central California, central Utah, and north-central New Mexico. In winter, descends to lower elevations (4,000 to 7,000 feet) but remains in the same general geographic area.

STATUS: Common.

HABITAT: Prefers barren, rocky or grassy areas and cliffs among glaciers or above timberline for breeding habitat. In winter, descends to lower elevation open habitat such as fields, cultivated lands, brushy areas, and areas of human habitation.

SPECIAL HABITAT REQUIREMENTS: Talus or cliffs for nesting.

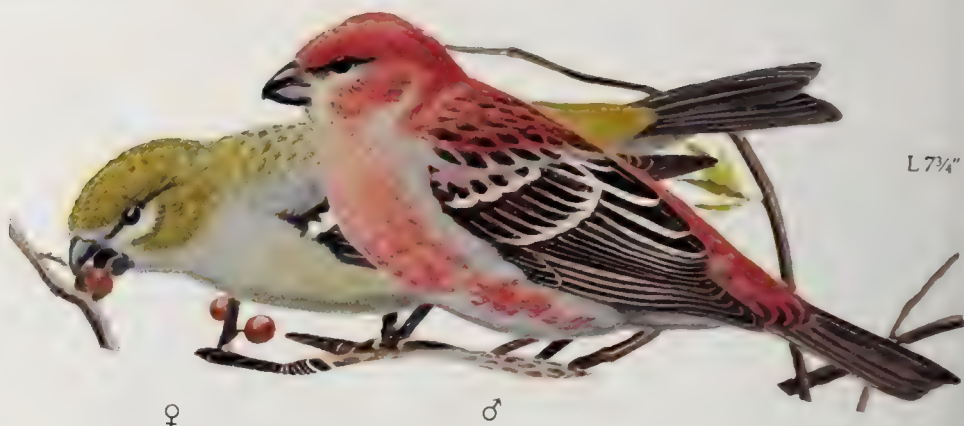
NEST: Nests in the cracks or holes of cliffs that offer protection. Builds a bulky nest of grasses and dry stalks of various herbaceous materials, lining it with fine grass and feathers.

FOOD: Consumes a diet that consists of vegetable material (more than 75 percent), mainly small seeds of alpine plants. Occasionally eats leaves and fruiting capsules and also consumes insects that are frozen in snow, as well as small insects found on the ground or in vegetation.

REFERENCES: French 1959, Johnson 1965.

Pine Grosbeak

Pinicola enucleator



RANGE: Breeds from western and central Alaska and northern Yukon east to northern Quebec and northern Labrador, south to central California and northern New Mexico, and, east of the Rockies, to northern Alberta, southern Ontario, and central Maine. Winters from central Alaska and southern Mackenzie east to Labrador and south throughout the breeding range; in invasion years occurs farther south.

STATUS: Locally common.

HABITAT: Inhabits coniferous forests near timberline in the western mountains, and northern spruce-fir forests up to treeline in Canada and Alaska. Also occurs in spruce stands bordering bogs, barren areas with clumps of dwarf spruce and tamarack, and mixed coniferous and deciduous woodlands. Prefers stands with large trees and low to intermediate canopy cover, usually near the edge of an open area or along a forest border.

SPECIAL HABITAT REQUIREMENTS: Coniferous forest of spruce-fir or pine.

NEST: Constructs nest in thick foliage near the end of a horizontal bough in conifers, often spruce, sometimes in underbrush. May place nest low in a conifer or up to 35 feet above the ground.

FOOD: Primarily eats buds and seeds of a variety of coniferous and deciduous trees, picked and gleaned from trees or from the ground. Also forages on some spiders and insects in spring and summer.

REFERENCES: Bent 1968a, Blake in Bent 1968a, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979, Taber in Bent 1968a, Verner and Boss 1980.

Purple Finch

Carpodacus purpureus



RANGE: Breeds from northern British Columbia, southern Yukon, and northern and central Alberta east to central Ontario and Newfoundland south to Baja California, and, east of the Great Plains, to central Minnesota, northern Ohio, West Virginia, and southeastern New York. Winters from southwestern British Columbia south to Baja California, and from southern Manitoba east to Newfoundland, south to Texas, the Gulf Coast, and Florida.

STATUS: Common.

HABITAT: Generally inhabits coniferous forest edge, open mixed woodlands, and evergreen plantations. Also occurs in conifers in parks and residential areas. In winter, commonly congregates around houses with feeding stations, roosting in dense evergreens or thickets.

NEST: In the East, places nest on a horizontal branch of a conifer, especially spruce, but occasionally in a deciduous tree or shrub. In the West, commonly nests in both deciduous and coniferous trees, preferably near water. Often locates nest near tree tops, up to 40 feet above the ground.

FOOD: During winter and spring, primarily eats seeds, while in late spring and summer adds insects and wild and cultivated fruits to diet. Gleans much of its food from the branches of trees and shrubs.

REFERENCES: Bent 1968a, DeGraff et al. 1980, Forbush and May 1955, Johnsgard 1979.

Cassin's Finch

Carpodacus cassinii



RANGE: Resident in western United States, in the mountains of the Pacific States, Idaho, and Montana, south into New Mexico and Arizona. Extends into Canada to breed, south into Mexico in winter.

STATUS: Common in western conifers.

HABITAT: Inhabits conifer forests, up to lodgepole pine type, with low to intermediate canopy cover; frequents forest edges more than interiors. In winter, moves to shrubby, bushy areas, as well as open areas with scattered trees.

SPECIAL HABITAT REQUIREMENTS: Conifer forests.

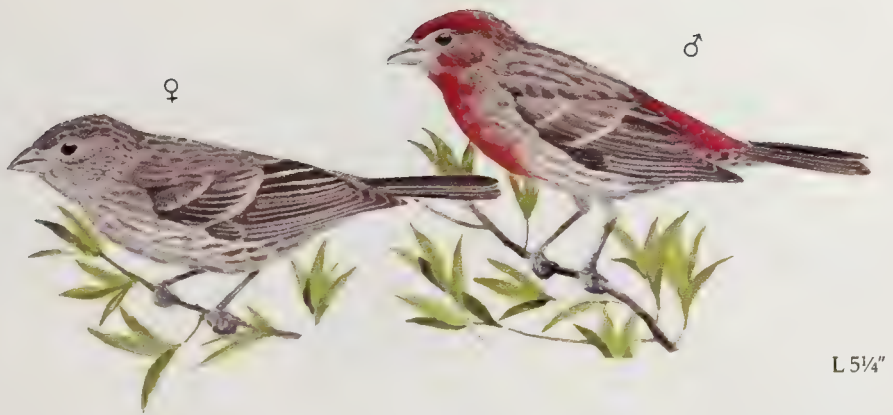
NEST: Nests in large conifers, near the ends of limbs quite high above the ground. Usually constructs nest of twigs, wood stems, rootlets, and lichen, and lined with hair and rootlets and sometimes bark.

FOOD: Primarily eats vegetable material, preferring buds, berries, and seeds, particularly those of conifers. Also eats some animal material, but only incidentally.

REFERENCES: Samson 1976, Verner and Boss 1980.

House Finch

Carpodacus mexicanus



RANGE: Breeds in disjunct distribution throughout most of the western United States, south into Texas and Mexico, and in the northeastern part of the United States, north of the Carolinas, into New England. Winters throughout the breeding range in the west and south into the Appalachian Mountains.

STATUS: Abundant. Expanding range in the East.

HABITAT: Inhabits rural, suburban, and urban yards, parks, farms, and open woodlands, as well as wooded areas with large openings, chaparral, and arid shrublands.

NEST: Builds nests in a variety of sites, including tree cavities, and in dense outer foliage of trees and shrubs. In the East, generally chooses conifers, locating nest about 20 feet above the ground. Usually constructs nest with a variety of local grass and other available vegetation.

FOOD: Forages on the ground for a variety of vegetative material, including seeds and fruits. Also forages in domestic fruit trees, sometimes doing considerable damage. Consumes widely varying kinds of foods, depending on local availability; includes some insects.

REFERENCES: DeGraff et al. 1980, Evenden 1957, Terres 1980.

Red Crossbill

Loxia curvirostra



RANGE: Resident from southern Alaska to Newfoundland, through southern Canada, and south to the northern Great Lakes area. Also from the Pacific states over to the Rocky Mountains, south into parts of Mexico. Wanders irregularly during the nonbreeding season.

STATUS: Locally common in conifer forests.

HABITAT: Inhabits coniferous and mixed coniferous-deciduous forests, humid pine-oak associations, and lowland pine savannah. Prefers forests with low canopy cover and is highly nomadic in response to changes in conifer seed production.

SPECIAL HABITAT REQUIREMENTS: Conifer forests with abundant seed production.

NEST: Builds saddled nest well out on a branch or in a cluster of conifer leaves 5 to 80 feet above the ground. Nests during all months when suitable seed crops are available, but mostly from February through June.

FOOD: Feeds primarily on seeds of conifer trees, plus seeds of deciduous trees in summer. Also eats insects during spring and summer.

REFERENCES: Forbush and May 1955, Griscom 1937, Snyder 1954.

White-winged Crossbill

Loxia leucoptera



RANGE: Resident from northeastern Alaska, south to the Pacific Northwest, throughout most of southern Canada, the eastern coast of Canada, and northern New England.

STATUS: Irregular.

HABITAT: Inhabits boreal forests, leaving them only when food is scarce.

SPECIAL HABITAT REQUIREMENTS: Conifer forests.

NEST: Builds a deep, saucer-shaped nest composed of lichens and twigs on branches of conifer trees. Frequently locates nest in a spruce tree, sometimes relatively close to the ground (2 to 70 feet). May breed during any month of the year, but mostly from January to May.

FOOD: Consumes a variety of foods, but seems to prefer seeds of Norway spruce and hemlock. Also eats insects, seeds of other conifers and deciduous trees, and some fruits.

REFERENCES: Forbush and May 1955, Terres 1980.

Common Redpoll

Carduelis flammea



RANGE: Breeds in the northern Arctic region from northern Alaska to Baffin Island, and south to northern British Columbia, and east to Newfoundland. Resident in southern part of the breeding range. Winters from Alaska and northern Saskatchewan east to Newfoundland and south to about mid-United States.

STATUS: Irregular.

HABITAT: Inhabits open fields with scattered small spruces or other trees, or small shrubs in the north circumpolar region. In winter, forms large flocks and moves erratically, occasionally to the edge of forests.

SPECIAL HABITAT REQUIREMENTS: Open field sites with perch areas

NEST: Generally places nest 3 to 7 feet above the ground, either in a dwarf tree or shrub or on the ground in open tundra. Conceals nest in vegetation, generally near lakes or ponds.

FOOD: Gleans seeds from birches, alders, pines, willows, and shrubs. Also forages on the ground for seeds of grasses, forbs, and trees, and for insects. Moves during winter to find sources of food.

REFERENCES: Forbush and May 1955, Grinnell 1943.

Hoary Redpoll

Carduelis hornemanni



RANGE: Breeds in western and northern Alaska, northern Yukon, northern and east-central Mackenzie, southern Victoria Island, Keewatin, northeastern Manitoba, Southampton Island, and northern Quebec. Also on Ellesmere, Bylot, and northern Baffin Islands, and in northern Greenland. Winters in the breeding range (except extreme northern areas) and south, irregularly, to southern Canada, and Montana to northern Illinois, New York, and New England.

HABITAT: Breeds in shrubby areas, including sparse, low vegetation in open tundra. In winter, inhabits open areas, fields, and open woodlands.

NEST: Builds nest with dry grass, rootlets, and willow down or feathers; places it in low shrubs such as willow or dwarf birch and often over water.

FOOD: Mostly eats plant materials, especially seeds, but some insects and larvae in summer. Forages on the ground, and gleans food from branches and leaves of shrubs.

REFERENCES: Bent 1968.

Pine Siskin

Carduelis pinus



RANGE: Breeds from central Alaska south through the Western United States and east across Canada to Newfoundland. Winters throughout Eastern and Southern United States from New England, the Great Lakes, and the Northern Plains States, south into Mexico. Resident in the southern Rocky Mountains, southwestern deserts, and the Pacific Coast.

STATUS: Irregularly common in large flocks.

HABITAT: Generally inhabits coniferous forests, and prefers those with low to intermediate canopy cover. Less numerous in second-growth alders, aspen, and broadleaf trees along the fringes of coniferous forests. Very social, forms flocks with other species.

SPECIAL HABITAT REQUIREMENTS: Coniferous forests.

NEST: Generally locates nest on a conifer branch, often in the shelter of another small branch and usually 15-35 feet above the ground.

FOOD: An opportunistic feeder that gleans food from foliage, bark of conifers, and from the ground. Also eats seeds, some berries, and a wide variety of insects.

REFERENCES: Forbush and May 1955, Weaver and West 1943, Terres 1980.

Lesser Goldfinch

Carduelis psaltria



RANGE: Resident from southwestern Washington, western Oregon, northern California, northern Utah, northern Colorado, northwestern Oklahoma, and central and southern Texas south to Baja California and South America.

STATUS: Common.

HABITAT: Generally inhabits scattered trees, woodland edge, second growth, open fields, pastures, and human habitation. Often found in drier foothill regions, in the deserts, and up to 7,300 feet in elevation and usually near water.

SPECIAL HABITAT REQUIREMENTS: Scattered trees and nearby water.

NEST: Saddles nest on a branch of a shrub or tree. Generally locates nest in dense foliage, 2 to 30 feet above the ground. Sometimes nests in loose colonies.

FOOD: Often forages in large flocks throughout the year, gleaning food from or near the ground; rarely feeds in tree crowns. Eats seeds, fruits, flowers, and other plant material, as well as small quantities of insects.

REFERENCES: Coutlee 1968, Linsdale 1957, Verner and Boss 1980.

Lawrence's Goldfinch

Carduelis lawrencei



RANGE: Breeds from central California south to southern California, northwestern Baja California, and western Arizona. Winters from north-central California, central Arizona, southwestern New Mexico, and western Texas south to northern Baja California, southern Arizona, and northern Sonora.

STATUS: Locally common.

HABITAT: Inhabits oak woodlands, chaparral, riparian woodlands, pinyon-juniper associations, and weedy areas in arid regions, usually near water.

SPECIAL HABITAT REQUIREMENTS: Scattered oak trees and water.

NEST: Prefers to nest in lichen-infested blue oaks that grow close together on dry slopes. Also nests in sycamores, and will often nest in small colonies. Locates nests about 20 feet above the ground in the forks of tree branches, usually 3 to 6 feet from the top of a main branch.

FOOD: Primarily eats seeds, gleaning them from foliage and the ground. Mostly eats weed seeds, but also shrub seeds and insects.

REFERENCES: Coutlee 1968, Linsdale 1957, Verner and Boss 1980.

American Goldfinch

Carduelis tristis



RANGE: Breeds from southern British Columbia and north-central Alberta east to central Ontario and southwestern Newfoundland, and south to California, southern Colorado, northeastern Texas, central Alabama, and South Carolina. Winters from southern British Columbia, the northern United States, southern Ontario, and Nova Scotia south to Mexico, the Gulf Coast, and southern Florida.

STATUS: Common.

HABITAT: Frequents habitats with thistles or cattails, such as open weedy fields, farmyards, swamps, pastures with scattered trees, and forest edges. In the West, inhabits riparian areas, especially those with willows present along streams, ditches, and ponds.

SPECIAL HABITAT REQUIREMENTS: Open weedy fields and scattered woody growth for nesting.

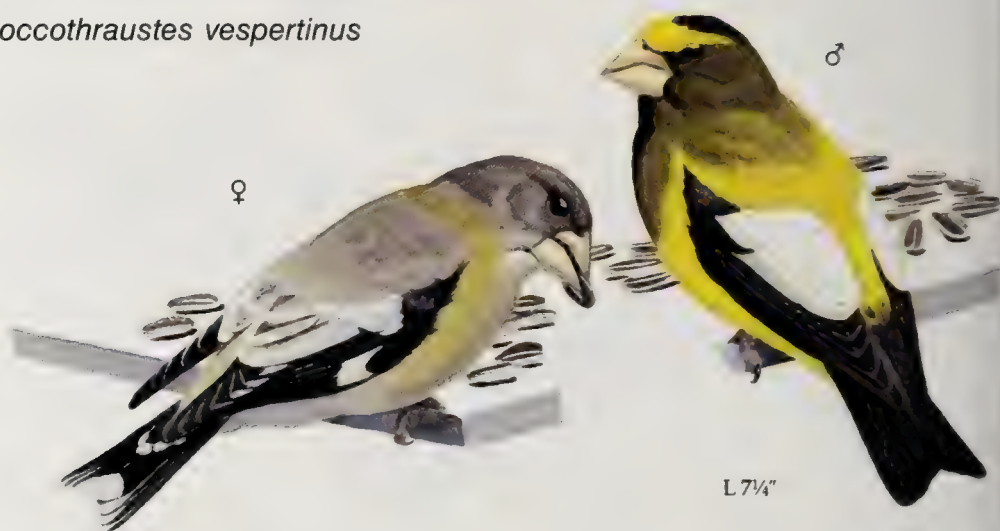
NEST: Usually builds nest in a cluster of upright branches or on a horizontal limb of a wide variety of trees or shrubs, typically 5 to 15 feet above the ground. Delays nesting until there is an abundant supply of seeds, particularly those of composites and thistles, to feed the young.

FOOD: Primarily eats seeds from a variety of plants, especially those in the composite family, as well as some insects in spring and summer, fruits, and succulent vegetation. Gleans food from the tips of weed stalks, the ground, and plants.

REFERENCES: Coutlee 1968, DeGraff et al. 1980, Forbush and May 1955, Holcomb 1969, Johnsgard 1979, Stokes 1950, Tyler in Bent 1968a.

Evening Grosbeak

Coccothraustes vespertinus



RANGE: Breeds from southwestern and north-central British Columbia to Nova Scotia and south, in the mountains, to central California, west-central and eastern Nevada, southeastern Arizona, southern New Mexico, the Mexican highlands, and, east of the Rocky Mountains, to Minnesota, Michigan, and Massachusetts. Winters throughout the breeding range sporadically south to southern California, southern Arizona, the Gulf Coast, and central Florida.

STATUS: Locally abundant.

HABITAT: Favors coniferous forests (primarily spruce and fir), throughout most of its range, often extending into areas where trees are quite sparse and into mixed forests. In winter, forms large flocks and may move downslope to oak or pine-oak habitats, parks, and around towns.

SPECIAL HABITAT REQUIREMENTS: Conifers.

NEST: Usually places nest on a horizontal limb of a conifer, 20 to 100 feet above the ground. Builds a shallow cup, usually in a dense cluster of leaves near the end of a branch.

FOOD: Eats seeds, fruits, and buds from a variety of trees and shrubs. In summer, the diet includes insects. Picks vegetable matter from the branches and the ground; gleans insects from branches or hawks them in the air.

REFERENCES: Forbush and May 1955, Verner and Boss 1980.

House Sparrow

Passer domesticus



L 5¼"

RANGE: First introduced from Europe in 1850, became established several years later. Now resident throughout most of North America, up to the edge of the tundra and south into Central America.

STATUS: Abundant.

HABITAT: Prefers to stay in the neighborhood of human dwellings; avoids large forests or other habitat far from human habitation. During winter, roosts in sheltered places such as open sheds and unoccupied buildings, under eaves or thick vines, or in a variety of holes and crevices.

NEST: Constructs nest with grass, string, and any locally available material, in cavities, crevices, open areas under eaves, on ledges of buildings, and in trees or shrubs. Nests in colonies in some areas.

FOOD: Consumes a wide variety of food, most of which is gleaned from the ground; also eats fruits from trees. Eats a variety of insects, vegetables, fruits, seeds, grains, and garbage. Is considered a pest around farms and feedlots, where it eats livestock feeds.

REFERENCES: DeGraff et al. 1980, Forbush and May 1955, Summers-Smith 1958, 1963.

Eurasian Tree Sparrow

Passer montanus



L 5"

RANGE: Introduced from Europe and established in St. Louis, Missouri, in 1870; now also found in east-central Missouri and western Illinois.

STATUS: Locally common.

HABITAT: Occurs in residential areas, farmlands, fields, and open woodland around St. Louis, where it was introduced in 1870. It is far less aggressive than its relative the house sparrow, but has slowly expanded its range to western Illinois.

NEST: Nests in natural cavities, crevices, and woodpecker holes, but appears to be a weak competitor for available nesting sites.

FOOD: Feeds primarily on the ground on weed seeds, insects, and waste grain. (Little information is available on food habits.)

REFERENCES: Bent 1958, Scott et al. 1977, Van Benthuyzen in Farrand 1983c.

BIRD/COVER-TYPE MATRICES

We have attempted to summarize bird use of the major forest types, grasslands, and deserts of the United States. We have indicated bird use of wetland and other open habitats commonly encountered within forests, and conversely, in wooded habitats within deserts and grasslands, but have not emphasized coastal habitats. This publication is primarily intended to serve as a reference for forest and rangeland managers.

Information provided in the following matrices was compiled from many sources. The 20 habitat matrices for the eastern and western forest types are based upon the forest cover type groups in "Forest cover types of the United States and Canada," F. H. Eyre, editor, Society of American Foresters, Washington, D.C., 1980. The habitat matrices presented for the Great Plains are based upon regions as described in "Land resource regions and major land resource areas of the United States," Soil Conservation Service, U.S. Department of Agriculture Handbook 296, Washington, D.C., 1981.

Nonforest habitat types within these broad forest cover types and Plains regions, and their use by birds in both the breeding and non-breeding seasons, were developed from the following:

"Management of southern forests for nongame birds," R. M. DeGraaf, technical coordinator, General Technical Report SE-14, Southeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture, Asheville, NC, 1978

"Nongame bird habitat management in the coniferous forests of the western United States," R. M. DeGraaf, technical coordinator, General Technical Report PNW-64, Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Portland, OR, 1978

"Management of north-central and northeastern forests for nongame birds," R. M. DeGraaf, technical coordinator, General Technical Report NC-51, North Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture, St. Paul, MN, 1979

"Management of western forests and grasslands for nongame birds," R. M. DeGraaf, technical coordinator, General Technical Report INT-86, Intermountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Ogden, UT, 1980

"New England wildlife: habitat, natural history, and distribution," R. M. DeGraaf and D. D. Rudis, General Technical Report NE-108, Northeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture, Broomall, PA, 1986

"Guide to bird habitats of the Ozark Plateau," K. E. Evans and R. A. Kirkman, General Technical Report NC-68, North Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture, St. Paul, MN, 1981

"Bird-habitat relationships on southeastern forest lands," P. B. Hamel, H. E. LeGrand, Jr., M. R. Lennartz, and S. A. Gauthreaux, Jr., General Technical Report SE-22, Southeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture, Asheville, NC, 1982

"Birds of the Great Plains," P. A. Johnsgard, University of Nebraska Press, Lincoln, NB, 1979

"Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington," J. W. Thomas, technical editor, Agriculture Handbook 553, Forest Service, U.S. Department of Agriculture, Washington, DC, 1979

"California wildlife and their habitats; western Sierra Nevada," J. Verner and A. S. Boss, technical coordinators, General Technical Report PSW-37, Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Berkeley, CA, 1980; and many unpublished reports provided by USDA Forest Service regional offices and colleagues.

Eastern Forest Cover Type Groups

Eastern White-Red-Jack Pine. Eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), or jack pine (*Pinus banksiana*) composes most of the stocking. The northeastern and Lake States pine types all occur as essentially pure stands, usually on lighter soils. Eastern white pine occurs from the Canadian Maritime Provinces, across the Lake States to Manitoba, and down the Appalachian Mountains to Georgia. It is shade-tolerant and also occurs as a scattered tree in other types, and on many soils. Red pine is most extensive in the Lake States and southern Ontario, and also extends east to New England, Quebec, and the Maritime Provinces, where it usually occurs on small outwash areas, rocky slopes, or hilltops. It is shade-intolerant, and occurs in even-age stands. Jack pine is mainly found in the Lake States; it characteristically originates after fire and is a short-lived, intolerant pioneer on dry, sandy soils.

Red Spruce-Balsam Fir. Red spruce (*Picea rubens*) or balsam fir (*Abies balsamea*) composes most of the stocking. These species frequently occur together from the Maritimes and adjacent Quebec, northern New England, New York, and the Appalachians. Either may be pure or compose a majority of the stocking; paper birch (*Betula papyrifera*), aspen (*Populus tremuloides* and *P. grandidentata*), red maple (*Acer rubrum*), eastern white pine, and northern white cedar (*Thuja occidentalis*) are common associates. Red spruce is long-lived and shade-tolerant; disturbance creates conditions favorable for establishment of balsam fir.

Longleaf Pine-Slash Pine. Longleaf pine (*Pinus palustris*) or slash pine (*P. elliottii*) composes a majority of the stocking. This type occurs on the Gulf and Atlantic coastal plains from Louisiana to South Carolina, on a range of sites from sandy ridges to poorly drained flatwoods. Excluding fire allows slash pine to become established, and hardwoods and shrubs commonly proliferate. Where longleaf pine stands are treated with prescribed fire, an open understory results.

Loblolly Pine-Shortleaf Pine. Loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines together compose the majority of the stocking. Loblolly pine predominates except on drier sites; the type occurs from Delaware south along the Atlantic coastal plain and Piedmont to Florida and west along the Gulf coastal plain to east Texas. Typically found on moist sites, it spreads to drier sites if fire is controlled. The type is succeeded by upland oaks.

Oak-Pine. Upland oaks and pines (usually loblolly or shortleaf) each comprise 25 percent of the stocking. Oak and pine types generally occur from east Texas to Georgia on upland sites on the Gulf coastal plain and Piedmont, and north in smaller areas through the Appalachians to include table mountain pine (*P. pungens*)-oak, Virginia pine (*P. virginiana*)-oak, and pitch pine (*P. resinosa*)-oak types.

Oak-Hickory. Upland oaks and hickories (*Carya* spp.) compose most of the stocking, and pines constitute less than 25 percent of the stocking. Oak-hickory forests occur across a wide geographic range from Texas, Missouri, and Iowa to southern New England, with many oak and other hardwood species involved under various physiographic conditions.

Oak-Gum-Cypress. In these bottomland forests of the lower Mississippi River Valley and those of its major tributaries from the Ohio River south, tupelo (*Nyssa*), blackgum (*N. sylvatica*), sweetgum (*Liquidambar styraciflua*), oak (*Quercus*), or bald cypress (*Taxodium distichum*), singly or in combination, compose most of the stocking; pines contribute less than 25 percent of the stocking.

Elm-Ash-Cottonwood. Elm (*Ulmus*), ash (*Fraxinus*), cottonwood (*Populus deltoides*), or red maple compose most of the stocking in these forests. Common associates in river bottoms (especially the Missouri River drainage) are sycamore (*Platanus*) and willow (*Salix*). On uplands, including those in Lake States, western New York, and southern New England, common associates are red maple (*Acer rubrum*) and American beech (*Fagus grandifolia*).

Northern Hardwoods. Sugar (*Acer saccharum*) or red maple, American beech, or yellow birch (*Betula alleghaniensis*), singly or in combination, compose most of the stocking. The northern hardwood

type group varies geographically in its composition. It extends from the Maritimes through Wisconsin and south through the central Appalachians. Sugar maple is characteristic of the type group. Beech is absent in much of its western extent and on wetter sites in the East, where red maple and yellow birch also become common. Balsam fir and red spruce are common associates in the Northeast, aspen is common throughout; northern red oak (*Quercus rubra*), white ash (*Fraxinus americana*), eastern white pine, paper birch, and eastern hemlock (*Tsuga canadensis*) are commonly associated in the central and southern parts of the range, where the type is often called mixed woods.

Aspen-Birch. Quaking and bigtooth aspens or paper birch compose a majority of the stocking. Aspen and paper birch are transcontinental in distribution. Both are pioneer types that establish after fire and clearcutting. Aspen is unique in that almost all stands regenerate from root suckers. The type is short-lived and is succeeded on dry sites by red pine, red maple, or oaks; on intermediate sites by white pine; on moist fertile sites by northern hardwoods; and on the wettest sites by balsam fir. Paper birch is succeeded by spruce-fir in the northern parts of its range and by northern hardwoods and eastern hemlock on well-drained, fertile sites elsewhere.

Western Forest Cover Type Groups

Douglas-fir. Douglas-fir (*Pseudotsuga menziesii*) composes most of the stocking. Common associates are western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), true firs (*Abies*), redwood (*Sequoia sempervirens*), ponderosa pine (*Pinus ponderosa*), and larch (*Larix*). The type group predominates in the Pacific Northwest, but also occurs (decreasing southward) throughout the Rocky Mountains south to northern New Mexico.

Hemlock-Sitka Spruce. Western hemlock and/or Sitka spruce (*Picea sitchensis*) compose most of the stocking. Common associates include Douglas-fir, silver fir (*Abies amabilis*), and western redcedar. The type comprises the coastal forests of Washington and Oregon.

Redwood. Redwood (*Sequoia sempervirens*) composes most of the stocking. The type is restricted to the California fog belt, extending from southernmost Oregon south along the Pacific Coast to the Santa Lucia Mountains. The type extends inland to the reaches of coastal fogs. Common associates are Douglas-fir, grand fir (*Abies grandis*), and tanoak (*Lithocarpus densiflorus*).

Ponderosa Pine. Ponderosa pine composes most of the stocking. Common associates in the western part of the range (California, Oregon)

include Jeffrey (*P. jeffreyi*), and sugar (*P. lambertiana*) pines; to the north, Douglas-fir and incense-cedar (*Libocedrus decurrens*); to the east, limber (*P. flexilis*), Arizona (*P. ponderosa* var. *arizonica*), and Chihuahua (*P. biophylla* var. *chihuahuana*) pines; and throughout, white fir (*Abies concolor*). The type is generally distributed to the west, north, and east of the Great Basin and the deserts of the Southwest.

Western White Pine-Larch. Western white pine (*Pinus monticola*) composes most of the stocking. The type attains its best development in northern Idaho and northwestern Montana. Common associates include western redcedar, larch, white fir, Douglas-fir, lodgepole pine (*P. contorta*), and Engelmann spruce (*Picea engelmannii*). Such admixtures produce the "mixed conifer" type, as it is known locally. Western larch (*Larix occidentalis*) comprises a plurality of the stocking in some areas between the Columbia River in eastern Washington and the west slopes of the Rocky Mountains in Montana. Common associates are Douglas-fir, grand fir, western redcedar, and western white pine.

Lodgepole Pine. Lodgepole pine composes most of the stocking; the mid-elevation type occurs to 11,000 feet in the Rocky Mountains, to 11,500 feet in California, and to 6,000 feet in Oregon and Washington. Best development is on moist, sandy, or gravelly loam. Common associates are subalpine fir (*Abies lasiocarpa*), western white pine, Engelmann spruce, aspen, and larch.

Fir-Spruce. The true firs, Engelmann spruce, or Colorado blue spruce (*Picea pungens*) compose most of the stocking. Common associates are lodgepole pine and, at high elevation, mountain hemlock (*Tsuga mertensiana*).

Aspen-Hardwoods. Aspen (*Populus tremuloides*) or red alder (*Alnus rubra*) compose a majority of the stocking. The aspen type is the most common and extensive hardwood type in the western United States. It occurs primarily at middle elevations on a variety of sites in the Rocky Mountain cordillera, where it is usually succeeded by interior Douglas-fir. Aspen is usually first to dominate burns and other disturbed areas, where it produces even-aged stands. Where conifer seed sources are absent, aspen may exist as a virtual climax, where it vegetatively reproduces repeatedly, developing into all-aged stands.

All western aspen communities have an herbaceous understory, commonly forbs, but sometimes grasses and sedges. In the northern portion of the type range in the West, willows, common bearberry, and buffaloberry are common understory shrubs. Farther south, snowberry, chokecherry, and western serviceberry are more common.

Red alder is essentially coastal and the most important hardwood of the Pacific Northwest; best growth is on moist, rich, loamy bottomlands.

Chaparral. Chaparral consists of heavily branched, dwarfed trees or shrubs, commonly evergreens, whose canopy at maturity covers at least 50 percent of the ground. Common constituent plants include oaks (*Quercus*), Mountain-mahogany (*Cercocarpus*), silktassel (*Garrya*), ceanothus (*Ceanothus*), manzanita (*Arctostaphylos*), and chamise (*Adlenostoma*).

Pinyon-Juniper. Pinyon pines (primarily *P. edulis*, *P. cembroides*, *P. monophylla*) and junipers (primarily *Juniperus osteosperma*, *J. deppeana*, and *J. monosperma*) compose most of the stocking. This type is widely distributed throughout the semiarid West, usually on dry, shallow, rocky soils of mesas, benches, and canyon walls.

Eastern Open, Wetland, Plains, Deserts, and Other Nonforest Habitats

Field, Glade, Orchard. Primarily grass, hayfields, abandoned agricultural land, and fruit orchards with grassy ground cover.

Pasture, Wet or Sedge Meadow. Agricultural lands that are too wet, steep, or rocky for crops; meadows dominated by grasses or sedges (*Carex* spp.) with soils that are saturated or seasonally flooded.

Fresh Marsh, Pond. Palustrine and lacustrine wetlands, permanently flooded, containing emergents such as cattails (*Typha*), bullrushes (*Scirpus*), rushes (*Juncus*), and floating-leaved plants: spatterdock (*Nuphar*) and water lily (*Nymphaea*).

Wooded Swamp, Bog, Shrub Swamp. Palustrine, forested wetlands, either needle-leaved evergreen or broad-leaved deciduous; dominant plants are Atlantic white-cedar (*Chamaecyparis thyoides*), black spruce (*Picea mariana*), or red maple. Wooded swamps are seasonally or permanently flooded; bogs are permanently flooded.

Lake, Stream, River. Stratified lacustrine wetlands; permanently flowing watercourses of any width.

Sand Pine, Scrub Oak. Southeastern and southern woodlands on droughty, infertile, coarse-textured or sandy soils that support any of the scrub oaks (*Q. laevis*, *Q. incana*, *Q. marilandica*, or *Q. stellata* var. *margaretta*) or sand pine (*Pinus clausa*).

Pocosins. Bay-swamp, and pond pine (*Pinus serotina*) woodlands with boggy soils in which broadleaf evergreens predominate: black gum (*Nyssa sylvatica* var. *biflora*), persea (*Persea barbonia*), magnolia (*Magnolia virginiana*), gordonia (*Gordonia lasianthus*) and associates, of pond pine, Atlantic white-cedar.

Everglades, Mangroves. Palustrine wetlands in southern Florida that are semi-permanently flooded, dominated by saw grass (*Cladium amaicense*); estuarine, intertidal wetlands dominated by mangrove (*Rhizophora*).

Alpine Tundra, Krummholtz. Elevated slopes above timberline characterized by low, shrubby, slow-growing woody plants and a ground cover of boreal lichens, sedges, and grasses; the transition zone from subalpine forest to alpine tundra characterized by dwarfed, wind-sheared trees.

Great Plains Habitats

Gulf Prairies and Marshes. Moderate to tall dense open grasslands dominated by seacoast bluestem (*Andropogon littoralis*) and coastal sacahuista (*Spartina spartinae*).

East Texas Prairies, Cross Timbers, Pineywoods, and Post Oak Savanna. Open grassy savanna to dense brushland occurring in north-central Texas; pine-hardwood forest and grazing lands of east Texas; midgrass prairie dominated by little bluestem (*Andropogon scoparius*) and shin oak (*Quercus mohriana*).

South Texas Shrub-Grassland. Vegetation ranges from desert grass-shrub vegetation in west Texas to mixed oak savanna in the eastern Edwards Plateau region to open grassland on the Rio Grande plain.

Southern Plains. Open to moderately dense short grasslands occurring from southeastern Colorado and central Oklahoma south through eastern New Mexico and Texas panhandle. Natural vegetation is characterized by grama (*Bouteloua*) and buffalo grass (*Buchloe*).

Central Plains. Grasslands ranging from short grasses in the West to tall grasses in the East. Includes the region from southeastern Wyoming and northeastern Colorado east through Indiana.

Northern Plains. Plains region from north-central Montana and northwestern Minnesota south to southeastern Wyoming and northwestern Iowa. Area supports grassland vegetation dominated by western wheatgrass (*Agropyron smithii*) and needlegrass (*Stipa*) in the West and by little bluestem in the East.

Wetland and Riparian Habitats. All Great Plains wetland and riparian habitats, including marshes, ponds, lakes, streams, stock ponds, and woodlands associated with wetlands.

Shelterbelts and Woodlots. Planted bands of trees that serve as windbreaks to protect fields or farmsteads; other wooded areas surrounded by agricultural lands.

Pine-Oak, Brushy Woodland, Badlands-Juniper. Includes dry woodlands of pines and oaks with or without a brushy understory. Badlands-juniper region is largely devoid of vegetation but may have scattered junipers on suitable sites.

Southwestern and Western Nonforested Habitats

Relict Conifer Forest, Madrean Evergreen Woodland. Warm-temperate forests and woodlands in the Southwest. Relict conifer forests consist of small populations of cypress (*Cupressus*) and closed-cone pines, bishop pine (*Pinus muricata*), and knobcone pine (*P. attenuata*), restricted to canyons and suitable slopes along drainages. Madrean evergreen woodland is composed primarily of evergreen oaks but includes madrean pines.

Aspen. Mid-elevation sites in the Great Basin consisting of pure or nearly pure stands of quaking aspen.

Great Basin Shrubsteppe. Open to dense stands of shrubs and low trees, including big sagebrush (*Artemisia tridentata*), saltbush (*Atriplex confertifolia*), greasewood (*Sarcobatus vermiculatus*), or creosote bush (*Larrea divaricata*).

Sonoran Desert Scrub. Open to dense vegetation of shrubs, low trees, and succulents dominated by paloverde (*Cercidium microphyllum*), pricklypear (*Opuntia* spp.), and giant saguaro (*Cereus giganteus*).

Chihuahuan Desert Scrub. Open stands of creosote bush and large succulents (*Ferocactus pringlei*, *Echinocactus platyacanthus*) in southern New Mexico and southwest Texas.

Mohave Desert Scrub. Located between the Great Basin desert scrub and the Sonoran desert scrub, it is intermediate between them, sharing plant species of both but containing the endemic arboreal leaf succulent, Joshua tree (*Yucca brevifolia*).

Desert Riparian Deciduous Woodland, Marsh. Woodlands, especially of cottonwoods, that occur where desert streams provide sufficient moisture for a narrow band of trees and shrubs along the margins.

Annual Grasslands, Farms. Grasslands dominated by wild oat (*Avena* spp.), ripgut brome (*Bromus rigidus*), soft chess (*Bromus mollis*), four clover (*Medicago hispida*), and filaree (*Erodium* spp.) with less than 5 percent woody cover.

River, Riparian Woodland, Subalpine Marsh. Occurs at elevations where stream conditions provide sufficient permanent moisture for emergent plants, or for a narrow band of deciduous trees and shrubs; at low elevation characterized by cottonwood and sycamore, at mid-elevation by white alder (*Alnus rhombifolia*) and bigleaf maple (*Acer macrophyllum*), and at high elevation by willow.

Mountain and Alpine Meadows. Sedges (*Carex*) and grasslike plants (*Heleocharis*, *Scirpus*) above treeline.

Table 1 —Birds occurring in eastern forest types

Bird Species	White-red-jack pine	Spruce-fir	Longleaf-slash pine	Loblolly-shortleaf pine	Oak-pine	Oak-hickory	Oak-gum-cypress	Elm-ash-cottonwood	Maple-beech-birch	Aspen-birch
Double-crested Cormorant							X			
Anhinga							X			
American Bittern							X			
Least Bittern							X			
Great Blue Heron							X	X		
Great Egret							X			
Snowy Egret							X			
Little Blue Heron							X			
Cattle Egret							X			
Green-backed Heron							X	X		
Black-crowned Night-Heron							X			
Yellow-crowned Night-Heron							X			
Glossy Ibis							X			
White-faced Ibis							X			
Wood Duck	X	X					X	X	X	
American Black Duck								X		
Gadwall								X		
Ring-necked Duck	X	X							X	
Common Goldeneye	X	X						X	X	
Bufflehead								X	X	
Hooded Merganser	X	X				X	X	X	X	X
Common Merganser	X	X				X		X	X	X
Black Vulture			X	X	X	X	X			
Turkey Vulture	X		X	X	X	X	X	X	X	
Osprey							X			
American Swallow-tailed Kite			X		X		X			
Mississippi Kite				X	X		X			
Bald Eagle	X	X	X	X	X		X	X	X	
Sharp-shinned Hawk	X	X	X	X	X	X	X	X	X	X
Cooper's Hawk	X	X	X	X	X	X	X	X	X	X
Northern Goshawk	X	X			X	X			X	X
Red-shouldered Hawk	X		X	X		X	X	X	X	X
Broad-winged Hawk	X	X	X	X	X	X			X	X
Short-tailed Hawk							X			
Red-tailed Hawk	X	X	X	X	X	X		X	X	X
Golden Eagle	X	X			X	X			X	X
American Kestrel	X	X	X	X	X	X		X	X	X
Merlin	X	X	X	X						
Peregrine Falcon	X	X	X	X	X	X		X	X	X
Spruce Grouse		X								

(Continued)

Table 1 —Birds occurring in eastern forest types—continued

Bird Species	White-red-jack pine	Spruce-fir	Longleaf-slash pine	Loblolly-shortleaf pine	Oak-pine	Oak-hickory	Oak-gum-cypress	Elm-ash-cottonwood	Maple-beech-birch	Aspen-birch
Ruffed Grouse	X	X			X	X			X	X
Wild Turkey	X		X	X	X	X	X	X	X	X
Northern Bobwhite	X		X	X	X	X				
Yellow Rail		X								
King Rail							X			
Virginia Rail								X		
Sora							X			
Purple Gallinule							X			
Common Moorhen							X	X		
Limpkin							X			
Solitary Sandpiper								X		
Spotted Sandpiper								X		
Upland Sandpiper				X	X	X				
Common Snipe							X	X		
American Woodcock	X	X	X	X	X	X	X	X	X	X
Rock Dove			X	X	X	X	X			
Mourning Dove	X	X	X	X	X	X	X		X	X
Common Ground-Dove			X	X	X	X				
Black-billed Cuckoo	X	X			X	X		X	X	X
Yellow-billed Cuckoo	X		X	X	X	X	X	X	X	X
Common Barn-Owl			X	X	X	X				
Eastern Screech-Owl	X	X	X	X	X	X	X	X	X	X
Great Horned Owl	X	X	X	X	X	X	X	X	X	X
Northern Hawk-Owl		X								X
Burrowing Owl			X	X	X	X				
Barred Owl	X	X		X		X	X	X	X	
Great Gray Owl		X								X
Long-eared Owl	X	X		X	X	X				
Boreal Owl		X							X	
Northern Saw-whet Owl	X	X			X	X			X	X
Common Nighthawk	X	X	X	X	X	X	X	X	X	X
Chuck-will's-widow			X	X	X	X				
Whip-poor-will	X	X	X	X	X	X	X	X	X	X
Chimney Swift	X	X	X	X	X	X	X	X	X	X
Ruby-throated Hummingbird	X	X	X	X	X	X	X	X	X	X
Belted Kingfisher	X	X			X	X	X	X	X	X
Red-headed Woodpecker			X	X	X	X	X	X		
Red-bellied Woodpecker			X	X	X	X	X	X		
Yellow-bellied Sapsucker	X	X	X	X	X	X	X	X	X	X
Downy Woodpecker	X	X	X	X	X	X	X	X	X	X

(Continued)

Table 1 —Birds occurring in eastern forest types—continued

Bird Species	White-red-jack pine	Spruce-fir	Longleaf-slash pine	Loblolly-shortleaf pine	Oak-pine	Oak-hickory	Oak-gum-cypress	Elm-ash-cottonwood	Maple-beech-birch	Aspen-birch
Hairy Woodpecker	X	X	X	X	X	X	X	X	X	X
Red-cockaded Woodpecker			X	X	X					
Three-toed Woodpecker		X								
Black-backed Woodpecker		X								
Northern Flicker	X	X	X	X	X	X	X	X	X	X
Pileated Woodpecker	X	X	X	X	X	X	X	X	X	X
Olive-sided Flycatcher	X	X							X	X
Eastern Wood-Pewee	X	X	X	X	X	X	X	X	X	X
Yellow-bellied Flycatcher	X	X							X	
Acadian Flycatcher					X	X	X	X		
Alder Flycatcher	X	X						X	X	X
Willow Flycatcher						X	X	X	X	X
Least Flycatcher	X	X				X		X	X	X
Eastern Phoebe	X	X	X	X	X	X	X	X	X	X
Great Crested Flycatcher	X	X	X	X	X	X	X	X	X	
Eastern Kingbird	X		X	X	X	X		X	X	X
Purple Martin	X	X	X	X	X	X	X	X	X	X
Tree Swallow	X	X	X	X			X	X	X	X
Northern Rough-winged Swallow	X	X	X	X	X	X		X	X	X
Bank Swallow	X	X			X	X		X	X	X
Cliff Swallow	X	X		X	X		X	X	X	X
Barn Swallow	X	X	X	X	X	X	X	X	X	X
Gray Jay		X							X	
Blue Jay	X	X	X	X	X	X	X	X	X	X
American Crow	X	X	X	X	X	X	X	X	X	X
Fish Crow			X	X	X		X			
Common Raven	X	X			X	X		X	X	X
Black-capped Chickadee	X	X		X	X	X		X	X	X
Carolina Chickadee	X		X	X	X	X	X			
Boreal Chickadee		X							X	
Tufted Titmouse	X		X	X	X	X	X	X		
Red-breasted Nuthatch	X	X	X	X	X	X			X	
White-breasted Nuthatch	X	X	X	X	X	X	X	X	X	X
Brown-headed Nuthatch			X	X	X					
Brown Creeper	X	X	X	X	X	X	X	X	X	X
Carolina Wren	X		X	X	X	X	X	X		
Bewick's Wren					X	X				
House Wren	X	X	X	X	X	X	X	X	X	X
Winter Wren	X	X	X	X	X	X	X	X	X	X
Marsh Wren							X	X		

(Continued)

Table 1 —Birds occurring in eastern forest types—continued

Bird Species	White-red-jack pine	Spruce-fir	Longleaf-slash pine	Loblolly-shortleaf pine	Oak-pine	Oak-hickory	Oak-gum-cypress	Elm-ash-cottonwood	Maple-beech-birch	Aspen-birch
Golden-crowned Kinglet	X	X	X	X	X	X	X	X	X	X
Ruby-crowned Kinglet	X	X	X	X	X		X	X	X	
Blue-gray Gnatcatcher			X	X	X	X	X	X		X
Eastern Bluebird	X		X	X	X	X		X	X	X
Veery	X	X				X		X	X	X
Gray-cheeked Thrush		X								
Swainson's Thrush	X	X							X	X
Hermit Thrush	X	X	X	X	X		X	X	X	X
Wood Thrush	X	X		X	X	X	X	X	X	X
American Robin	X	X	X	X	X	X	X	X	X	X
Gray Catbird	X	X	X	X	X	X	X	X	X	X
Northern Mockingbird			X	X	X	X	X	X		
Brown Thrasher	X	X	X	X	X	X	X	X	X	X
Water Pipit							X			
Bohemian Waxwing										X
Cedar Waxwing	X	X	X	X	X	X	X	X	X	X
Northern Shrike	X	X							X	X
Loggerhead Shrike	X		X	X	X	X	X			X
European Starling	X			X	X	X	X	X	X	X
White-eyed Vireo				X	X	X	X	X	X	X
Solitary Vireo	X	X	X	X	X		X		X	X
Yellow-throated Vireo			X	X		X	X	X	X	
Warbling Vireo						X	X	X	X	
Philadelphia Vireo									X	X
Red-eyed Vireo	X	X		X	X	X	X	X	X	X
Bachman's Warbler							X			
Blue-winged Warbler						X			X	X
Golden-winged Warbler					X	X			X	X
Tennessee Warbler	X	X							X	X
Orange-crowned Warbler		X					X			
Nashville Warbler	X	X							X	X
Northern Parula	X	X		X	X	X	X	X	X	X
Yellow Warbler	X	X				X	X		X	X
Chestnut-sided Warbler	X	X			X	X			X	X
Magnolia Warbler	X	X							X	
Cape May Warbler	X	X								
Black-throated Blue Warbler	X	X				X			X	X
Yellow-rumped Warbler	X	X	X	X	X	X	X	X	X	X
Black-throated Green Warbler	X	X		X	X		X		X	
Blackburnian Warbler		X				X			X	

(Continued)

Table 1 —Birds occurring in eastern forest types—continued

Bird Species	White-red-jack pine	Spruce-fir	Longleaf-slash pine	Loblolly-shortleaf pine	Oak-pine	Oak-hickory	Oak-gum-cypress	Elm-ash-cottonwood	Maple-beech-birch	Aspen-birch
Yellow-throated Warbler	X		X	X	X	X	X	X		
Pine Warbler	X		X	X	X				X	
Prairie Warbler	X		X	X	X	X	X			X
Palm Warbler	X	X	X	X						
Bay-breasted Warbler	X	X								
Blackpoll Warbler		X								
Cerulean Warbler					X	X		X		
Black-and-white Warbler	X	X	X	X	X	X	X	X	X	X
American Redstart	X	X				X	X	X	X	X
Prothonotary Warbler							X	X		
Worm-eating Warbler				X	X	X	X			
Swainson's Warbler	X						X			
Ovenbird	X	X			X	X	X	X	X	X
Northern Waterthrush	X	X					X	X	X	
Louisiana Waterthrush					X	X	X	X		
Kentucky Warbler					X	X	X	X		
Mourning Warbler	X	X							X	X
Common Yellowthroat	X	X	X	X	X	X	X	X	X	X
Hooded Warbler				X	X	X	X			
Wilson's Warbler		X								
Canada Warbler	X	X						X	X	X
Yellow-breasted Chat	X		X	X	X	X	X	X		
Summer Tanager			X	X	X	X	X			
Scarlet Tanager	X				X	X	X	X	X	X
Northern Cardinal	X		X	X	X	X	X	X	X	
Rose-breasted Grosbeak	X	X				X		X	X	X
Blue Grosbeak				X	X	X	X			
Indigo Bunting	X		X	X	X	X	X	X	X	X
Painted Bunting				X		X	X			
Dickcissel				X	X	X				
Rufous-sided Towhee	X		X	X	X	X	X	X	X	X
Bachman's Sparrow			X	X	X	X				
American Tree Sparrow	X	X		X	X	X		X	X	X
Chipping Sparrow	X	X	X	X	X	X			X	X
Lark Sparrow				X		X				
Fox Sparrow	X	X	X	X			X			
Song Sparrow	X	X	X	X	X	X	X	X	X	X
Lincoln's Sparrow							X			
Swamp Sparrow		X								
White-throated Sparrow	X	X	X	X	X	X	X	X	X	X

(Continued)

Table 1 —Birds occurring in eastern forest types—continued

Bird Species	White-red-jack pine	Spruce-fir	Longleaf-slash pine	Loblolly-shortleaf pine	Oak-pine	Oak-hickory	Oak-gum-cypress	Elm-ash-cottonwood	Maple-beech-birch	Aspen-birch
White-crowned Sparrow				X	X	X				
Dark-eyed Junco	X	X	X	X	X	X		X	X	X
Red-winged Blackbird							X	X		
Rusty Blackbird		X					X	X		
Brewer's Blackbird				X	X	X				
Common Grackle	X									
Brown-headed Cowbird	X	X	X	X	X	X	X	X	X	X
Orchard Oriole					X	X	X	X		
Northern Oriole						X	X	X	X	X
Pine Grosbeak	X	X								
Purple Finch	X	X	X	X	X	X		X	X	X
House Finch								X		
Red Crossbill	X	X		X	X					
White-winged Crossbill	X	X			X					
Pine Siskin	X	X	X	X	X	X			X	
American Goldfinch										X
Evening Grosbeak	X	X			X	X		X	X	

Table 2 —Birds occurring in eastern nonforest habitats
(exclusive of Great Plains)

Bird Species	Field, glade, orchard	Pasture, wet or sedge meadows	Fresh marsh, pond	Wooded swamp, bog, shrub swamp	Lake, stream, river	Sand pine-scrub oak	Pocosins	Everglades, mangroves, tropical hardwoods	Alpine tundra, krummholz
Common Loon					X				
Pied-billed Grebe			X	X	X			X	
Horned Grebe			X		X				
Red-necked Grebe			X		X				
Double-crested Cormorant					X			X	
Anhinga			X		X			X	
American Bittern		X	X		X			X	
Least Bittern		X	X					X	
Great Blue Heron		X	X		X		X	X	
Great Egret		X	X				X	X	
Snowy Egret		X	X				X	X	
Little Blue Heron			X				X	X	
Cattle Egret	X	X	X				X	X	
Green-backed Heron		X	X	X	X		X	X	
Black-crowned Night-Heron			X	X	X		X	X	
Yellow-crowned Night-Heron			X	X	X		X	X	
Glossy Ibis			X				X	X	
Fulvous Whistling-Duck			X					X	
Canada Goose	X	X	X		X				
Wood Duck			X	X	X		X	X	
Green-winged Teal		X	X					X	
American Black Duck		X	X	X	X				
Mottled Duck			X					X	
Mallard	X	X	X		X				
Northern Pintail			X						
Blue-winged Teal			X					X	
Northern Shoveler			X					X	
Gadwall			X	X					
American Wigeon		X	X		X				
Redhead			X		X				
Ring-necked Duck			X	X	X				
Greater Scaup					X				
Lesser Scaup			X		X				
Common Goldeneye			X		X				
Bufflehead			X		X				
Hooded Merganser			X	X	X				
Common Merganser			X		X				
Red-breasted Merganser			X		X				
Ruddy Duck			X		X				
Black Vulture	X	X				X	X	X	

(Continued)

Table 2 —Birds occurring in eastern nonforest habitats
(exclusive of Great Plains)—Continued

Bird Species	Field, glade, orchard	Pasture, wet or sedge meadows	Fresh marsh, pond	Wooded swamp, bog, shrub swamp	Lake, stream, river	Sand pine-scrub oak	Pocosins	Everglades, mangroves, tropical hardwoods	Alpine tundra, krummholz
Turkey Vulture	X	X				X	X	X	
Osprey			X		X		X	X	
American Swallow-tailed Kite			X					X	
Black-shouldered Kite	X								
Snail Kite								X	
Mississippi Kite						X	X		
Bald Eagle			X		X			X	
Northern Harrier		X	X				X	X	
Sharp-shinned Hawk				X				X	
Cooper's Hawk	X	X							
Red-shouldered Hawk				X			X	X	
Broad-winged Hawk								X	
Short-tailed Hawk								X	
Red-tailed Hawk	X	X				X	X	X	
Rough-legged Hawk	X	X	X						
Golden Eagle	X	X							
American Kestrel	X	X				X	X	X	
Merlin	X	X	X				X	X	
Peregrine Falcon	X	X	X		X		X	X	X
Ring-necked Pheasant	X	X							
Ruffed Grouse	X								
Wild Turkey	X	X				X			
Northern Bobwhite	X					X			
Yellow Rail		X	X					X	
Black Rail			X				X	X	
King Rail			X					X	
Virginia Rail			X					X	
Sora			X					X	
Purple Gallinule			X					X	
Common Moorhen				X		X			X
American Coot			X		X			X	
Limpkin				X				X	
Sandhill Crane		X	X					X	
Piping Plover					X				
Killdeer		X	X		X			X	
Greater Yellowlegs		X							
Lesser Yellowlegs		X							
Solitary Sandpiper			X	X	X				
Spotted Sandpiper					X			X	
Upland Sandpiper		X							

(Continued)

Table 2 —Birds occurring in eastern nonforest habitats
(exclusive of Great Plains)—Continued

Bird Species	Field, glade, orchard	Pasture, wet or sedge meadows	Fresh marsh, pond	Wooded swamp, bog, shrub swamp	Lake, stream, river	Sand pine-scrub oak	Pocosins	Everglades, mangroves, tropical hardwoods	Alpine tundra, krummholz
Common Snipe		X	X	X				X	
American Woodcock	X	X	X	X			X	X	
Common Tern					X				
Black Tern			X		X				
Rock Dove	X	X							
White-crowned Pigeon								X	
Mourning Dove	X	X				X	X	X	
Common Ground-Dove	X					X	X	X	
Yellow-billed Cuckoo						X	X	X	
Mangrove Cuckoo								X	
Smooth-billed Ani								X	
Common Barn-Owl	X	X	X			X		X	
Eastern Screech-Owl		X	X				X	X	
Great Horned Owl	X	X	X	X		X	X	X	
Snowy Owl	X	X	X						
Burrowing Owl						X			
Barred Owl				X			X	X	
Great Gray Owl	X	X	X	X					
Long-eared Owl	X	X	X						
Short-eared Owl	X	X	X					X	
Common Nighthawk	X	X	X		X	X		X	
Chuck-will's-widow						X		X	
Whip-poor-will	X							X	
Chimney Swift	X	X	X		X				
Ruby-throated Hummingbird	X	X						X	
Belted Kingfisher			X		X			X	
Red-headed Woodpecker	X	X				X	X		
Red-bellied Woodpecker	X			X		X	X	X	
Yellow-bellied Sapsucker	X					X	X	X	
Downy Woodpecker	X			X		X	X	X	
Hairy Woodpecker			X		X	X			
Northern Flicker	X	X				X		X	
Pileated Woodpecker								X	
Olive-sided Flycatcher				X					
Eastern Wood-Pewee	X						X		
Yellow-bellied Flycatcher				X					
Acadian Flycatcher				X			X		
Alder Flycatcher				X					
Willow Flycatcher	X								
Least Flycatcher	X			X					

(Continued)

Table 2 —Birds occurring in eastern nonforest habitats
(exclusive of Great Plains)—Continued

Bird Species	Field, glade, orchard	Pasture, wet or sedge meadows	Fresh marsh, pond	Wooded swamp, bog, shrub swamp	Lake, stream, river	Sand pine-scrub oak	Pocosins	Everglades, mangroves, tropical hardwoods	Alpine tundra, krummholtz
Eastern Phoebe	X	X		X		X	X	X	
Great Crested Flycatcher						X	X	X	
Western Kingbird								X	
Eastern Kingbird	X	X	X			X		X	
Gray Kingbird								X	
Scissor-tailed Flycatcher								X	
Horned Lark	X	X							
Purple Martin	X	X	X		X		X	X	
Tree Swallow	X	X	X	X	X			X	
Northern Rough-winged Swallow	X	X	X		X			X	
Bank Swallow	X	X	X		X				
Cliff Swallow	X	X	X		X				
Barn Swallow	X	X	X		X				
Gray Jay									X
Blue Jay	X	X		X		X	X	X	
Scrub Jay						X			
American Crow	X	X				X	X	X	
Fish Crow			X		X		X	X	
Common Raven		X							X
Black-capped Chickadee	X			X					X
Carolina Chickadee	X			X		X	X		
Boreal Chickadee				X					X
Tufted Titmouse	X			X			X	X	
Red-breasted Nuthatch				X		X	X		X
White-breasted Nuthatch	X			X			X		
Brown-headed Nuthatch						X	X	X	
Brown Creeper	X			X		X	X		
Carolina Wren	X	X	X	X		X	X	X	
Bewick's Wren	X	X							
House Wren	X	X		X		X	X	X	
Winter Wren				X			X		
Sedge Wren		X						X	
Marsh Wren		X	X					X	
Golden-crowned Kinglet				X		X	X		X
Ruby-crowned Kinglet				X		X	X	X	X
Blue-Gray Gnatcatcher				X			X	X	
Eastern Bluebird	X	X				X		X	
Veery				X					
Gray-cheeked Thrush									X
Hermit Thrush				X			X	X	

(Continued)

Table 2 —Birds occurring in eastern nonforest habitats
(exclusive of Great Plains)—Continued

Bird Species	Field, glade, orchard	Pasture, wet or sedge meadows	Fresh marsh, pond	Wooded swamp, bog, shrub swamp	Lake, stream, river	Sand pine-scrub oak	Pocosins	Everglades, mangroves, tropical hardwoods	Alpine tundra, krummholz
Wood Thrush				X			X		
American Robin	X	X		X		X	X	X	
Gray Catbird	X	X		X		X	X	X	
Northern Mockingbird	X	X				X	X	X	
Brown Thrasher	X	X				X	X	X	
Water Pipit	X	X			X				
Bohemian Waxwing	X								
Cedar Waxwing	X	X		X	X	X		X	
Northern Shrike	X	X							
Loggerhead Shrike	X	X				X		X	
White-eyed Vireo	X			X		X	X	X	
Solitary Vireo				X		X	X	X	
Yellow-throated Vireo				X	X		X	X	
Warbling Vireo	X	X	X	X	X				
Red-eyed Vireo	X	X		X			X		
Black-whiskered Vireo								X	
Bachman's Warbler							X		
Blue-winged Warbler	X	X							
Golden-winged Warbler	X	X							
Orange-crowned Warbler						X	X	X	
Nashville Warbler				X					
Northern Parula				X	X		X	X	
Yellow Warbler	X	X	X	X	X			X	
Chestnut-sided Warbler		X		X					
Magnolia Warbler									X
Cape May Warbler								X	X
Black-throated Blue Warbler								X	
Yellow-rumped Warbler				X		X	X	X	
Black-throated Green Warbler							X	X	
Yellow-throated Warbler						X	X	X	
Pine Warbler						X	X	X	
Prairie Warbler	X					X	X	X	
Palm Warbler		X		X		X	X	X	
Bay-breasted Warbler	X								
Blackpoll Warbler									X
Black-and-white Warbler				X		X	X	X	
American Redstart	X			X				X	
Prothonotary Warbler				X	X		X		
Worm-eating Warbler							X		
Swainson's Warbler							X		

(Continued)

Table 2 —Birds occurring in eastern nonforest habitats
(exclusive of Great Plains)—Continued

Bird Species	Field, glade, orchard	Pasture, wet or sedge meadows	Fresh marsh, pond	Wooded swamp, bog, shrub swamp	Lake, stream, river	Sand pine-scrub oak	Pocosins	Everglades, mangroves, tropical hardwoods	Alpine tundra, krummholtz
Ovenbird								X	
Northern Waterthrush				X			X	X	
Louisiana Waterthrush				X	X				
Kentucky Warbler				X	X				
Common Yellowthroat	X	X	X	X	X	X	X	X	
Hooded Warbler				X			X		
Wilson's Warbler				X					
Canada Warbler				X					
Yellow-breasted Chat	X	X	X	X		X	X	X	
Summer Tanager						X	X	X	
Northern Cardinal	X	X		X		X	X	X	
Rose-breasted Grosbeak	X								
Blue Grosbeak	X	X				X	X		
Indigo Bunting	X	X				X	X	X	
Painted Bunting						X	X	X	
Dickcissel	X							X	
Rufous-sided Towhee	X					X		X	
Bachman's Sparrow	X					X			
American Tree Sparrow	X	X	X						
Chipping Sparrow	X	X				X		X	
Field Sparrow	X					X			
Vesper Sparrow	X	X				X			
Lark Sparrow	X								
Savannah Sparrow	X	X	X			X	X	X	
Grasshopper Sparrow	X					X		X	
Henslow's Sparrow	X	X							
Le Conte's Sparrow	X	X	X						
Sharp-tailed Sparrow		X							
Fox Sparrow	X					X			
Song Sparrow	X	X	X				X	X	
Lincoln's Sparrow				X	X				
Swamp Sparrow		X	X	X			X	X	
White-throated Sparrow	X	X				X	X		
White-crowned Sparrow	X					X			
Dark-eyed Junco	X	X							X
Lapland Longspur	X	X							
Snow Bunting	X	X	X						
Bobolink	X	X							
Red-winged Blackbird	X	X	X	X	X		X	X	
Eastern Meadowlark	X					X		X	

(Continued)

Table 2 —Birds occurring in eastern nonforest habitats
(exclusive of Great Plains)—Continued

Bird Species	Field, glade, orchard	Pasture, wet or sedge meadows	Fresh marsh, pond	Wooded swamp, bog, shrub swamp	Lake, stream, river	Sand pine-scrub oak	Pocosins	Everglades, mangroves, tropical hardwoods	Alpine tundra, krummholz
Western Meadowlark	X								
Rusty Blackbird			X	X		X	X		
Brewer's Blackbird	X								
Boat-tailed Grackle								X	
Common Grackle	X	X	X	X	X	X	X	X	
Brown-headed Cowbird	X	X	X	X		X	X		
Orchard Oriole	X					X			
Northern Oriole	X	X		X	X			X	
Purple Finch	X						X		
House Finch	X								
Red Crossbill									X
Common Redpoll	X	X							
Pine Siskin	X	X					X		
American Goldfinch	X	X	X	X		X	X	X	
House Sparrow	X	X							

Table 3—Birds occurring in Great Plains habitats

Bird Species	Gulf prairies and marshes	East Texas prairies, cross timbers, pineywoods, and post oak savannah	South Texas shrub grassland	Southern plains	Central plains	Northern plains	Wetland and riparian habitats	Shelterbelts and woodlots	Pine-oak, brushy woodland, badlands/juniper
Common Loon	X						X		
Pied-billed Grebe	X						X		
Horned Grebe	X						X		
Red-necked Grebe							X		
Eared Grebe	X						X		
Western Grebe							X		
American White Pelican	X						X		
Double-crested Cormorant	X						X		
Anhinga	X						X		
American Bittern	X						X		
Least Bittern	X						X		
Great Blue Heron	X						X		
Great Egret	X						X		
Snowy Egret	X						X		
Little Blue Heron	X						X		
Cattle Egret	X	X	X	X	X		X		
Green-backed Heron	X						X		
Black-crowned Night-Heron	X						X		
Yellow-crowned Night-Heron	X						X		
Black-bellied Whistling-Duck	X								
Tundra Swan	X						X		
Greater White-fronted Goose	X						X		
Snow Goose	X						X		
Ross' Goose	X						X		
Canada Goose	X	X	X	X	X	X	X		
Wood Duck	X	X					X		
Green-winged Teal	X	X	X	X	X	X	X		
American Black Duck	X						X		
Mottled Duck	X								
Mallard	X	X	X	X	X	X	X		
Northern Pintail	X	X	X	X	X	X	X		
Blue-winged Teal	X						X		
Cinnamon Teal	X				X	X	X		
Northern Shovler	X						X		
Gadwall	X						X		
American Wigeon	X						X		
Canvasback	X						X		
Redhead	X						X		
Ring-necked Duck	X						X		
Greater Scaup	X						X		

(Continued)

Table 3—Birds occurring in Great Plains habitats—continued

Bird Species	Gulf prairies and marshes	East Texas prairies, cross timbers, pineywoods, and post oak savannah	South Texas shrub grassland	Southern plains	Central plains	Northern plains	Wetland and riparian habitats	Shelterbelts and woodlots	Pine-oak, brushy woodland, badlands/juniper
Lesser Scaup	X	X		X		X	X		
Common Goldeneye	X						X		
Bufflehead	X				X	X	X		
Hooded Merganser	X						X		
Common Merganser	X			X	X	X	X		
Red-breasted Merganser	X						X		
Ruddy Duck	X				X	X	X		
Black Vulture	X	X	X	X					
Turkey Vulture	X	X	X	X	X	X	X	X	X
Osprey							X		
Black-shouldered Kite	X								
Mississippi Kite	X	X	X	X			X		
Bald Eagle	X	X	X	X	X		X	X	X
Northern Harrier	X	X	X	X	X	X	X	X	X
Sharp-shinned Hawk	X	X	X	X	X	X	X	X	X
Cooper's Hawk	X	X	X	X	X	X	X	X	X
Northern Goshawk						X			
Harris' Hawk	X	X	X						
Red-shouldered Hawk	X	X	X				X		
Broad-winged Hawk	X	X					X	X	X
Swainson's Hawk	X	X	X	X	X	X	X	X	X
White-tailed Hawk	X		X						
Zone-tailed Hawk			X						
Red-tailed Hawk	X	X	X	X	X	X	X	X	X
Ferruginous Hawk	X	X	X	X	X	X			X
Rough-legged Hawk	X	X	X	X	X	X	X	X	X
Golden Eagle	X	X		X	X	X	X	X	X
American Kestrel	X	X	X	X	X	X	X	X	X
Merlin	X	X	X			X	X	X	X
Peregrine Falcon	X		X						X
Prairie Falcon	X		X			X			X
Plain Chachalaca			X						
Gray Partridge					X	X		X	
Ring-necked Pheasant					X	X	X	X	
Sage Grouse						X	X		
Greater Prairie-Chicken	X			X	X	X			
Lesser Prairie-Chicken			X						
Sharp-tailed Grouse					X	X		X	
Wild Turkey		X	X				X	X	X
Northern Bobwhite		X	X	X	X		X	X	X

(Continued)

Table 3—Birds occurring in Great Plains habitats—continued

Bird Species	Gulf prairies and marshes	East Texas prairies, cross timbers, pineywoods, and post oak savannah	South Texas shrub grassland	Southern plains	Central plains	Northern plains	Wetland and riparian habitats	Shelterbelts and woodlots	Pine-oak, brushy woodland, badlands/juniper
Scaled Quail			X	X	X				
Yellow Rail	X								
Black Rail	X						X		
Clapper Rail	X								
King Rail	X						X		
Virginia Rail	X						X		
Sora	X						X		
Purple Gallinule	X						X		
Common Moorehen	X						X		
American Coot	X			X	X	X	X		
Sandhill Crane	X						X		
Whooping Crane	X						X		
Black-bellied Plover	X						X		
Snowy Plover	X						X		
Piping Plover	X						X		
Killdeer	X		X	X	X	X	X		
Mountain Plover	X			X	X	X			
Black-necked Stilt	X						X		
American Avocet	X			X	X	X	X		
Greater Yellowlegs	X						X		
Lesser Yellowlegs	X						X		
Willet	X				X	X	X		
Spotted Sandpiper	X	X	X	X	X	X	X		
Upland Sandpiper				X	X	X	X		
Long-billed Curlew	X			X	X	X	X		
Marbled Godwit	X					X	X		
Ruddy Turnstone	X								
Red Knot	X								
Sanderling	X								
Western Sandpiper	X						X		
Least Sandpiper	X						X		
Short-billed Dowitcher	X						X		
Long-billed Dowitcher	X								
Common Snipe	X						X		
American Woodcock	X	X					X		
Wilson's Phalarope	X			X	X	X	X		
Franklin's Gull					X	X	X		
Bonaparte's Gull	X						X		
Ring-billed Gull	X				X	X	X		
California Gull						X	X		

(Continued)

Table 3—Birds occurring in Great Plains habitats—continued

Bird Species	Gulf prairies and marshes	East Texas prairies, cross timbers, pineywoods, and post oak savannah	South Texas shrub grassland	Southern plains	Central plains	Northern plains	Wetland and riparian habitats	Shelterbelts and woodlots	Pine-oak, brushy woodland, badland, and riparian
Herring Gull	X						X		
Caspian Tern	X						X		
Common Tern							X		
Forster's Tern	X						X		
Least Tern				X	X				
Black Tern							X		
Rock Dove		X	X	X	X	X		X	X
White-winged Dove	X		X						
Mourning Dove		X	X	X	X	X	X	X	X
Inca Dove		X	X						
Common Ground-Dove		X	X	X					
Black-billed Cuckoo						X	X	X	X
Yellow-billed Cuckoo	X	X	X				X	X	
Greater Roadrunner		X	X	X	X				X
Groove-billed Ani	X	X	X						
Common Barn-Owl		X	X	X	X	X	X	X	X
Eastern Screech-Owl		X	X	X	X	X	X	X	X
Great Horned Owl		X	X	X	X	X	X	X	X
Snowy Owl						X	X	X	
Burrowing Owl			X	X	X	X			
Barred Owl		X					X	X	
Long-eared Owl							X	X	X
Short-eared Owl	X	X	X	X	X	X	X		
Northern Saw-whet Owl							X	X	X
Lesser Nighthawk			X						
Common Nighthawk	X	X	X	X	X	X	X	X	X
Common Pauraque	X		X						
Common Poorwill			X	X	X	X			X
Chuck will's-widow	X	X					X	X	
Whip-poor-will	X						X	X	
Chimney Swift	X	X	X	X	X	X	X	X	
Buff-bellied Hummingbird			X						
Ruby-throated Hummingbird	X	X	X	X	X	X	X	X	
Black-chinned Hummingbird		X	X	X					
Broad-tailed Hummingbird			X				X	X	
Belted Kingfisher	X	X	X				X		
Green Kingfisher			X						
Red-headed Woodpecker	X	X	X	X	X	X	X	X	X
Golden-fronted Woodpecker	X		X	X			X		
Red-bellied Woodpecker		X							

(Continued)

Table 3—Birds occurring in Great Plains habitats—continued

Bird Species	Gulf prairies and marshes	East Texas prairies, cross timbers, pineywoods, and post oak savannah	South Texas shrub grassland	Southern plains	Central plains	Northern plains	Wetland and riparian habitats	Shelterbelts and woodlots	Pine-oak, brushy woodland, badlands/juniper
Yellow-bellied Sapsucker	X	X	X				X	X	
Ladder-backed Woodpecker			X	X			X	X	
Downy Woodpecker	X	X			X	X	X	X	X
Hairy Woodpecker	X	X			X	X	X	X	X
Red-cockaded Woodpecker		X							
Northern Flicker	X	X	X	X	X	X	X	X	X
Pileated Woodpecker							X		
Olive-sided Flycatcher							X		
Western Wood-Pewee			X	X			X	X	
Eastern Wood-Pewee		X	X				X	X	
Acadian Flycatcher	X	X	X				X		
Willow Flycatcher					X	X	X	X	X
Least Flycatcher							X	X	
Eastern Phoebe	X	X	X				X	X	
Say's Phoebe	X	X	X	X	X	X	X	X	X
Vermilion Flycatcher	X	X	X				X		
Ash-throated Flycatcher		X	X	X			X		
Great Crested Flycatcher	X	X	X	X	X	X	X	X	X
Brown-crested Flycatcher			X						
Couch's Kingbird			X						
Cassin's Kingbird			X	X	X		X	X	X
Western Kingbird	X	X	X	X	X	X	X	X	X
Eastern Kingbird	X	X	X	X	X	X	X	X	X
Scissor-tailed Flycatcher	X	X	X	X	X		X	X	
Horned Lark	X		X	X	X	X			
Purple Martin	X	X	X		X		X	X	
Tree Swallow	X				X		X	X	
Violet-green Swallow						X	X		
Northern Rough-winged Swallow	X		X	X	X	X	X		
Bank Swallow	X			X	X	X	X		
Cliff Swallow		X	X	X	X	X	X	X	
Barn Swallow	X	X	X	X	X	X	X	X	X
Blue Jay	X	X	X	X	X	X	X	X	X
Scrub Jay			X	X			X		
Black-billed Magpie				X	X	X	X	X	X
American Crow	X	X	X	X	X	X	X	X	X
Fish Crow	X								
Chihuahuan Raven			X	X					
Common Raven			X						X
Black-capped Chickadee					X	X	X	X	X

(Continued)

Table 3—Birds occurring in Great Plains habitats—continued

Bird Species	Gulf prairies and marshes	East Texas prairies, cross timbers, pineywoods, and post oak savannah	South Texas shrub grassland	Southern plains	Central plains	Northern plains	Wetland and riparian habitats	Shelterbelts and woodlots	Pine-oak, brushy woodland, <small>Local to the Great Plains</small>
Carolina Chickadee	X	X					X	X	
Tufted Titmouse	X	X	X	X			X	X	
Verdin			X	X			X		
Bushtit			X	X			X		
Red-breasted Nuthatch		X					X	X	X
White-breasted Nuthatch		X					X	X	X
Brown-headed Nuthatch		X							
Brown Creeper	X	X	X				X	X	X
Cactus Wren			X						
Rock Wren			X	X	X	X	X		X
Canyon Wren			X	X					
Carolina Wren	X	X	X				X		
Bewick's Wren		X	X	X	X		X	X	
House Wren	X	X	X				X	X	X
Winter Wren	X	X					X		
Sedge Wren	X				X	X	X		
Marsh Wren	X		X		X	X	X		
Golden-crowned Kinglet		X	X				X	X	X
Ruby-crowned Kinglet	X	X	X				X	X	X
Blue-gray Gnatcatcher	X	X	X				X	X	
Black-tailed Gnatcatcher			X						
Eastern Bluebird	X	X	X		X		X	X	
Veery	X					X	X	X	
Swainson's Thrush	X		X						
Hermit Thrush	X	X	X				X	X	
Wood Thrush		X					X		
American Robin	X	X	X	X	X	X	X	X	X
Gray Catbird	X	X	X		X	X	X	X	X
Northern Mockingbird	X	X	X				X	X	X
Sage Thrasher			X						
Brown Thrasher	X	X		X	X	X	X	X	X
Long-billed Thrasher	X		X						
Curve-billed Thrasher			X	X					
Water Pipit	X	X	X	X			X		
Sprague's Pipit	X	X	X	X			X	X	
Cedar Waxwing	X	X	X	X	X	X	X	X	X
Bohemian Waxwing						X			
Northern Shrike						X	X	X	
Loggerhead Shrike	X	X	X	X	X	X	X	X	X
European Starling	X	X	X	X	X	X	X	X	X

(Continued)

Table 3—Birds occurring in Great Plains habitats—continued

Bird Species	Gulf prairies and marshes	East Texas prairies, cross timbers, pineywoods, and post oak savannah	South Texas shrub grassland	Southern plains	Central plains	Northern plains	Wetland and riparian habitats	Shelterbelts and woodlots	Pine-oak, brushy woodland, badlands/juniper
White-eyed Vireo	X	X	X				X	X	
Bell's Vireo		X	X	X			X		X
Black-capped Vireo		X	X	X					
Solitary Vireo	X	X	X	X			X		
Yellow-throated Vireo	X	X	X				X	X	
Warbling Vireo	X	X	X				X	X	X
Red-eyed Vireo	X	X	X		X		X	X	X
Blue-winged Warbler					X		X	X	
Orange-crowned Warbler	X	X	X				X		X
Northern Parula	X	X	X				X		
Yellow Warbler		X	X	X			X	X	
Yellow-rumped Warbler	X	X	X	X	X	X	X	X	X
Golden-cheeked Warbler		X	X						
Yellow-throated Warbler	X	X	X				X		
Cerulean Warbler		X					X		
Black-and-white Warbler	X	X	X				X	X	X
American Redstart		X			X	X	X	X	
Prothonotary Warbler	X	X					X		
Worm-eating Warbler		X					X		
Swainson's Warbler		X					X		
Ovenbird	X						X		X
Northern Waterthrush							X		
Louisiana Waterthrush	X	X					X		
Kentucky Warbler		X					X	X	
Common Yellowthroat	X	X	X	X	X	X	X	X	X
Hooded Warbler		X					X		
Wilson's Warbler	X					X			
Yellow-breasted Chat	X	X	X	X		X	X	X	
Summer Tanager	X	X	X				X	X	
Scarlet Tanager							X	X	
Northern Cardinal	X	X	X		X		X	X	
Pyrrhuloxia			X						
Rose-breasted Grosbeak	X						X	X	
Black-headed Grosbeak							X	X	X
Blue Grosbeak		X	X	X	X		X	X	X
Lazuli Bunting				X	X	X	X	X	X
Indigo Bunting	X	X	X	X	X		X	X	X
Painted Bunting	X	X	X	X					
Dickcissel	X	X	X	X	X	X			
Olive Sparrow			X						

(Continued)

Table 3—Birds occurring in Great Plains habitats—continued

Bird Species	Gulf prairies and marshes	East Texas prairies, cross timbers, pineywoods, and post oak savannah	South Texas shrub grassland	Southern plains	Central plains	Northern plains	Wetland and riparian habitats	Shelterbelts and woodlots	Pine-oak, brushy woodland, badlands
Green-tailed Towhee			X	X	X			X	
Rufous-sided Towhee	X	X	X	X	X	X	X	X	X
Brown Towhee			X	X					
Bachman's Sparrow		X							
Cassin's Sparrow	X		X	X	X				
Rufous-crowned Sparrow		X	X	X					
American Tree Sparrow					X	X	X	X	X
Chipping Sparrow	X	X	X	X	X	X	X	X	X
Clay-colored Sparrow	X		X			X	X	X	
Brewer's Sparrow		X	X	X	X	X			
Field Sparrow	X	X	X	X	X	X	X	X	X
Vesper Sparrow	X	X	X	X	X	X			X
Lark Sparrow	X	X	X	X	X	X	X	X	X
Black-throated Sparrow			X	X					
Lark Bunting		X	X	X	X	X	X	X	X
Savannah Sparrow	X	X	X	X	X	X	X		
Baird's Sparrow			X			X			
Grasshopper Sparrow		X	X	X	X	X			X
Henslow's Sparrow	X	X			X				X
Le Conte's Sparrow	X	X	X			X	X	X	
Sharp-tailed Sparrow	X						X		
Seaside Sparrow	X								
Fox Sparrow	X	X	X	X		X	X	X	
Song Sparrow	X	X	X	X	X	X	X	X	X
Lincoln's Sparrow		X	X			X	X		
Swamp Sparrow	X	X	X	X			X	X	
White-throated Sparrow	X	X	X	X	X	X	X	X	X
White-crowned Sparrow	X	X	X	X		X	X	X	X
Harris' Sparrow		X	X	X	X	X	X		X
Dark-eyed Junco	X	X		X	X	X	X	X	X
McCown's Longspur	X			X		X			
Lapland Longspur				X	X	X			
Smith's Longspur		X			X				
Chestnut-collared Longspur				X	X	X			
Snow Bunting					X	X			
Bobolink					X	X	X		
Red-winged Blackbird	X	X	X	X	X	X	X	X	
Eastern Meadowlark	X	X	X	X	X	X	X		
Western Meadowlark	X	X	X	X	X	X		X	X
Yellow-headed Blackbird	X				X	X	X		X

(Continued)

Table 3—Birds occurring in Great Plains habitats—continued

Bird Species	Gulf prairies and marshes	East Texas prairies, cross timbers, pineywoods, and post oak savannah	South Texas shrub grassland	Southern plains	Central plains	Northern plains	Wetland and riparian habitats	Shelterbelts and woodlots	Pine-oak, brushy woodland, badlands/juniper
Dusty Blackbird	X	X	X				X		
Brewer's Blackbird	X	X	X	X	X	X	X		X
Great-tailed Grackle	X	X	X	X			X		
Coat-tailed Grackle	X								
Common Grackle	X	X	X	X	X	X	X	X	X
Brown-headed Cowbird	X	X	X	X	X	X	X	X	X
Orchard Oriole	X	X	X				X	X	
Northern Oriole	X	X	X	X	X	X	X	X	X
Purple Finch	X	X	X						
House Finch		X	X	X	X		X	X	X
Red Crossbill							X	X	
Common Redpoll						X			
Pine Siskin	X	X	X	X	X	X	X	X	
Lesser Goldfinch			X	X					
American Goldfinch	X	X	X	X	X	X	X	X	X
Evening Grosbeak					X	X	X	X	X
House Sparrow	X	X	X	X	X	X	X	X	X

Table 4 —Birds occurring in western forest types

Bird Species	Douglas-fir	Hemlock-Sitka spruce	Redwood	Ponderosa pine	Larch/white pine	Lodgepole pine	Fir-spruce	Aspen/hardwoods	Chaparral	Disjunct
Wood Duck		X	X	X	X		X	X		
Harlequin Duck		X			X					
Common Goldeneye	X	X			X					
Barrow's Goldeneye	X	X			X					
Bufflehead	X	X	X	X	X			X		
Hooded Merganser	X	X			X					
Common Merganser	X	X	X	X			X	X		
Turkey Vulture	X	X	X	X	X	X	X	X	X	
Osprey	X	X	X	X	X	X	X	X	X	
Black-shouldered Kite	X			X				X		
Bald Eagle	X	X	X	X	X	X	X	X	X	
Sharp-shinned Hawk	X	X	X	X	X	X	X	X	X	
Cooper's Hawk	X	X	X	X	X	X	X	X	X	
Northern Goshawk	X	X	X	X	X	X	X	X		
Red-shouldered Hawk	X			X				X		
Swainson's Hawk				X				X	X	
Red-tailed Hawk	X	X	X	X	X	X	X	X	X	
Rough-legged Hawk				X				X	X	
Golden Eagle	X	X	X	X	X	X	X	X	X	
American Kestrel	X	X	X	X	X	X	X	X	X	
Merlin	X	X	X	X	X	X	X	X	X	
Peregrine Falcon	X	X	X	X	X	X	X	X	X	
Prairie Falcon				X				X	X	
Chukar				X				X	X	
Spruce Grouse		X			X		X			
Blue Grouse	X	X	X	X	X	X	X	X		
Ruffed Grouse	X	X		X	X	X		X		
Wild Turkey	X			X	X	X	X	X	X	
California Quail	X	X	X	X			X	X	X	
Mountain Quail	X	X	X	X		X	X	X	X	
Marbled Murrelet	X	X								
Band-tailed Pigeon	X	X	X	X		X	X	X	X	
Mourning Dove	X	X	X	X		X	X	X	X	
Common Barn-Owl	X	X	X	X	X		X	X	X	
Flammulated Owl	X			X	X	X	X	X		
Western Screech-Owl	X	X	X	X		X		X	X	
Great Horned Owl	X	X	X	X	X	X	X	X	X	
Northern Pygmy-Owl	X	X	X	X	X	X	X	X	X	
Spotted Owl	X	X	X	X	X	X	X	X		
Barred Owl	X	X		X	X		X	X		

(Continued)

Table 4 —Birds occurring in western forest types—continued

Bird Species	Douglas-fir	Hemlock-Sitka spruce	Redwood	Ponderose pine	Larch/white pine	Lodgepole pine	Fir-spruce	Aspen/hardwoods	Chaparral	Pinyon-juniper
Great Gray Owl	X				X	X	X	X		
Long-eared Owl	X	X	X	X	X	X	X	X	X	X
Short-eared Owl				X				X	X	X
Pacifica Owl	X					X	X	X		
Northern Saw-whet Owl	X	X	X	X	X	X	X	X	X	X
Common Nighthawk	X	X		X			X	X	X	X
Common Poorwill	X			X			X	X	X	X
Whip-poor-will				X						
Black Swift	X	X					X	X		
Audubon's Swift	X	X	X	X	X	X	X	X		
White-throated Swift	X	X	X	X	X	X	X	X		X
Black-chinned Hummingbird	X	X	X	X	X		X	X	X	
Anna's Hummingbird	X	X	X	X			X	X	X	
Calliope Hummingbird	X			X	X	X	X	X		
Broad-tailed Hummingbird	X		X	X	X	X	X	X	X	
Rufous Hummingbird	X	X	X	X	X	X	X	X	X	X
Allen's Hummingbird	X	X	X	X		X	X	X	X	
Belted Kingfisher	X		X	X	X			X		X
Lewis' Woodpecker	X		X	X	X		X	X		
Acorn Woodpecker	X		X	X			X	X		
Yellow-bellied Sapsucker	X	X	X		X	X	X	X	X	
Red-breasted Sapsucker	X	X	X	X				X		
Williamson's Sapsucker	X		X	X	X	X	X	X		
Red-back Woodpecker									X	X
Nuttall's Woodpecker	X		X	X				X	X	X
Downy Woodpecker	X	X	X	X	X	X	X	X		X
Hairy Woodpecker	X	X	X	X	X	X	X	X		X
White-headed Woodpecker	X	X	X	X	X	X	X			
Three-toed Woodpecker	X	X		X	X	X	X			
Black-backed Woodpecker	X	X	X	X	X	X	X	X		
Northern Flicker	X	X	X	X	X	X	X	X	X	X
Pileated Woodpecker	X	X	X	X	X	X	X	X		
Olive-sided Flycatcher	X	X	X	X	X	X	X	X		
Western Wood-Pewee	X	X	X	X	X	X	X	X	X	X
Willow Flycatcher	X	X		X	X			X		X
Hammond's Flycatcher	X	X	X	X	X	X	X	X		
Dusky Flycatcher	X			X	X	X	X	X	X	X
Gray Flycatcher				X					X	X
Western Flycatcher	X	X	X	X	X	X	X	X		X
Black Phoebe				X				X	X	

(Continued)

Table 4 —Birds occurring in western forest types—continued

Bird Species	Douglas-fir	Hemlock-Sitka spruce	Redwood	Ponderosa pine	Larch/white pine	Lodgepole pine	Fir-spruce	Aspen/hardwoods	Chaparral
Say's Phoebe				X				X	X
Ash-throated Flycatcher				X				X	X
Brown-crested Flycatcher				X					X
Cassin's Kingbird				X					X
Western Kingbird				X					X
Purple Martin	X	X	X	X		X	X	X	
Tree Swallow	X	X	X	X	X	X	X	X	X
Violet-green Swallow	X	X	X	X	X	X	X	X	X
Northern Rough-winged Swallow	X						X	X	X
Cliff Swallow	X	X	X	X			X	X	X
Barn Swallow	X	X	X	X			X	X	X
Gray Jay	X	X	X	X	X	X	X	X	
Steller's Jay	X	X	X	X	X	X	X	X	
Scrub Jay	X		X	X				X	X
Pinyon Jay	X		X	X		X	X	X	X
Clark's Nutcracker	X		X	X	X	X	X	X	
Black-billed Magpie	X			X	X	X	X	X	
Yellow-billed Magpie								X	
American Crow	X			X		X	X	X	X
Common Raven	X	X	X	X	X	X	X	X	X
Black-capped Chickadee	X	X	X	X		X	X	X	
Mountain Chickadee	X	X	X	X	X	X	X	X	
Chestnut-backed Chickadee	X	X	X		X		X	X	
Plain Titmouse	X		X	X				X	X
Bushtit	X		X	X				X	X
Red-breasted Nuthatch	X	X	X	X	X	X	X	X	
White-breasted Nuthatch	X	X	X	X	X	X	X	X	
Pygmy Nuthatch	X			X	X	X	X	X	
Brown Creeper	X	X	X	X	X	X	X	X	
Rock Wren	X			X	X	X	X	X	X
Canyon Wren	X			X		X	X	X	X
Bewick's Wren	X		X	X			X	X	X
House Wren	X	X	X	X	X	X	X	X	X
Winter Wren	X	X	X	X	X	X	X	X	
American Dipper	X		X	X	X	X	X	X	
Golden-crowned Kinglet	X	X	X	X	X	X	X	X	X
Ruby-crowned Kinglet	X	X	X	X	X	X	X	X	X
Blue-gray Gnatcatcher	X		X	X				X	X
Western Bluebird	X		X	X	X	X	X	X	X
Mountain Bluebird	X			X	X	X	X	X	X

(Continued)

Table 4 —Birds occurring in western forest types—continued

Bird Species	Douglas-fir	Hemlock-Sitka spruce	Redwood	Ponderose pine	Larch/white pine	Lodgepole pine	Fir-spruce	Aspen/hardwoods	Chaparral	Pinyon-juniper
Townsend's Solitaire	X	X	X	X	X	X	X	X	X	X
Swainson's Thrush	X	X	X	X	X	X	X	X	X	X
Hermit Thrush	X	X	X	X	X	X	X	X	X	X
American Robin	X	X	X	X	X	X	X	X	X	X
Varied Thrush	X	X	X	X	X	X	X	X		
Wrentit	X		X	X				X	X	
Gray Catbird				X				X		X
Northern Mockingbird			X	X				X	X	X
Curve-billed Thrasher									X	X
California Thrasher									X	
Bohemian Waxwing	X	X	X	X		X	X	X		X
Cedar Waxwing	X	X	X	X			X	X	X	X
Phainopepla									X	X
Northern Shrike	X			X				X		X
Loggerhead Shrike	X			X				X	X	X
European Starling				X				X	X	X
Solitary Vireo	X	X	X	X	X	X	X	X	X	X
Hutton's Vireo	X	X	X	X			X	X	X	
Warbling Vireo	X	X	X	X		X	X	X	X	
Red-eyed Vireo	X			X				X		
Orange-crowned Warbler	X	X	X	X		X	X	X	X	X
Nashville Warbler	X	X	X		X		X	X		
Virginia's Warbler				X					X	X
Yellow Warbler	X	X	X	X	X	X	X	X	X	X
Yellow-rumped Warbler	X	X	X	X	X	X	X	X	X	X
Black-throated Gray Warbler				X	X			X	X	X
Townsend's Warbler	X	X	X	X	X	X	X	X		
Hermit Warbler	X	X	X	X		X	X	X		
Grace's Warbler	X			X						
Northern Waterthrush					X			X		
MacGillivray's Warbler	X	X	X	X	X	X	X	X	X	
Common Yellowthroat	X	X	X	X	X	X	X	X		
Wilson's Warbler	X	X	X	X	X	X	X	X		
Red-faced Warbler				X			X	X		
Painted Redstart				X				X		X
Yellow-breasted Chat				X	X			X	X	
Hepatic Tanager				X				X		
Summer Tanager				X				X		
Western Tanager	X	X	X	X	X	X	X	X	X	X
Black-headed Grosbeak	X	X	X	X	X		X	X	X	X

(Continued)

Table 4—Birds occurring in western forest types—continued

Bird Species	Douglas-fir	Hemlock-Sitka spruce	Redwood	Ponderosa pine	Larch/white pine	Lodgepole pine	Fir-spruce	Aspen/hardwoods	Chaparral	Pinon-juniper
Lazuli Bunting	X		X	X			X	X	X	X
Indigo Bunting				X						X
Green-tailed Towhee				X				X	X	X
Rufous-sided Towhee	X	X	X	X	X	X	X	X	X	X
Rufous-crowned Sparrow				X				X	X	
American Tree Sparrow	X			X						
Chipping Sparrow	X	X	X	X	X	X	X	X	X	X
Fox Sparrow	X	X	X				X	X	X	X
Song Sparrow	X	X	X	X			X	X	X	X
Lincoln's Sparrow	X	X	X			X	X	X		
Golden-crowned Sparrow	X	X	X				X	X	X	X
White-crowned Sparrow	X	X	X	X		X	X	X	X	X
Harris' Sparrow				X				X	X	
Dark-eyed Junco	X	X	X	X	X	X	X	X	X	X
Brewer's Blackbird	X			X			X	X	X	X
Northern Oriole	X	X	X	X	X		X	X	X	X
Scott's Oriole										X
Rosy Finch	X			X		X	X			
Pine Grosbeak	X	X		X	X	X	X	X		
Purple Finch	X	X	X		X			X		
Cassin's Finch	X	X	X	X	X	X	X	X		
House Finch	X	X	X	X	X	X	X	X	X	X
Red Crossbill	X	X	X	X	X	X	X			
White-winged Crossbill	X	X			X	X	X			
Common Redpoll								X		
Pine Siskin	X	X	X	X	X	X	X	X	X	X
Lesser Goldfinch			X	X				X	X	X
Lawrence's Goldfinch								X	X	
American Goldfinch	X	X	X	X				X	X	X
Evening Grosbeak	X	X	X	X	X	X	X	X	X	X

Table 5—Birds occurring in southwestern and western nonforest habitats

Bird Species	Great Basin shrubsteppe	Sonoran Desert scrub	Chihuahuan Desert scrub	Mojave Desert scrub	Desert riparian deciduous woodlands, marshes	Annual grasslands, farms	River, riparian woodlands, subalpine marshes	Mountain and alpine meadows	Relict conifer forests, madrean evergreen woodlands
Pied-billed Grebe					X		X		
Horned Grebe					X		X		
Red-tailed Grebe					X		X		
Western Grebe					X		X		
Double-crested Cormorant					X		X		
American Bittern					X		X		
Least Bittern					X				
Great Blue Heron					X	X	X	X	
Great Egret					X		X		
Snowy Egret					X		X		
Cattle Egret					X	X			
Green-backed Heron					X		X		
Black-crowned Night-Heron					X		X	X	
White-faced Ibis					X	X	X		
Black-bellied Whistling-Duck					X				
Tundra Swan					X	X	X	X	
Trumpeter Swan							X	X	
Greater White-fronted Goose						X	X		
Snow Goose					X	X	X		
Ross' Goose						X	X		
Canada Goose					X	X	X	X	
Wood Duck					X		X		
Green-winged Teal					X	X	X	X	
Mallard					X	X	X	X	
Northern Pintail					X	X	X	X	
Blue-winged Teal					X	X	X	X	
Cinnamon Teal					X	X	X	X	
Northern Shoveler					X	X	X	X	
Gadwall					X	X	X	X	
American Wigeon					X	X	X	X	
Canvasback					X		X		
Redhead					X		X		
Ring-necked Duck					X		X		
Greater Scaup							X		
Lesser Scaup					X	X	X		
Harlequin Duck							X		
Common Goldeneye					X		X		
Barrow's Goldeneye							X		
Bufflehead					X		X		
Hooded Merganser							X		

(Continued)

Table 5—Birds occurring in southwestern and western nonforest habitats—continued

Bird Species	Great Basin shrubsteppe	Sonoran Desert scrub	Chihuahuan Desert scrub	Mojave Desert scrub	Desert riparian deciduous woodlands, marshes	Annual grasslands, farms	River, riparian woodlands, subalpine marshes	Mountain and alpine meadows	Relict conifer forests, madrean evergreen
Common Merganser					X		X	X	
Red-breasted Merganser							X		
Ruddy Duck					X		X	X	
Black Vulture		X	X						
Turkey Vulture	X	X	X	X	X	X	X	X	
California Condor						X		X	
Osprey					X		X		
Black-shouldered Kite						X	X	X	
Bald Eagle	X				X	X	X	X	
Northern Harrier	X				X	X	X	X	
Sharp-shinned Hawk	X	X			X		X	X	
Cooper's Hawk	X						X	X	X
Northern Goshawk	X						X	X	
Common Black-Hawk					X				
Harris' Hawk		X	X		X				
Gray Hawk					X				
Red-shouldered Hawk						X	X		
Swainson's Hawk	X	X	X	X		X	X	X	
Zone-tailed Hawk					X		X		
Red-tailed Hawk	X	X	X	X	X	X	X	X	
Ferruginous Hawk	X	X	X	X					
Rough-legged Hawk	X	X	X	X		X		X	
Golden Eagle	X	X	X	X	X	X	X	X	
American Kestrel	X	X	X	X	X	X	X	X	X
Merlin	X	X	X	X	X	X	X		
Peregrine Falcon	X	X	X	X	X	X	X		X
Prairie Falcon	X	X	X	X	X	X	X	X	
Gray Partridge	X					X			
Chukar	X								
Ring-necked Pheasant	X					X	X		
Blue Grouse							X	X	
White-tailed Ptarmigan								X	
Ruffed Grouse							X		
Sage Grouse	X						X	X	
Sharp-tailed Grouse	X					X		X	
Wild Turkey	X	X			X		X		X
Montezuma Quail		X			X				X
Northern Bobwhite		X				X	X		
Scaled Quail		X	X			X			
Gambel's Quail	X	X	X	X	X				X

(Continued)

Table 5—Birds occurring in southwestern and western nonforest habitats—continued

Bird Species					Great Basin shrubsteppe	Sonoran Desert scrub	Chihuahuan Desert scrub	Mojave Desert scrub	Desert riparian deciduous woodlands, marshes	Annual grasslands, farms	River, riparian woodlands, subalpine marshes	Mountain and alpine meadows	Relict conifer forests, madrean evergreen woodlands
California Quail					X				X	X			
Mountain Quail					X						X	X	
Slapper Rail									X				
Virginia Rail									X		X	X	
Worm-eating Warbler									X		X	X	
Common Moorhen									X				
American Coot									X	X	X	X	
Sandhill Crane									X	X	X		
Whooping Crane									X				
White-tailed Deer					X	X	X	X	X	X	X	X	
Mountain Plover										X		X	
Black-necked Stilt									X		X		
American Avocet									X	X	X	X	
Greater Yellowlegs									X		X		
Willet									X		X		
Spotted Sandpiper									X	X	X	X	
Upland Sandpiper										X		X	
Long-billed Curlew									X	X	X	X	
Marbled Godwit										X	X	X	
Least Sandpiper									X	X	X		
Long-billed Dowitcher									X		X		
Common Snipe									X	X	X	X	
Wilson's Phalarope									X		X		
Franklin's Gull									X	X	X	X	
Ring-billed Gull									X	X	X		
California Gull									X	X	X		
Herring Gull									X		X		
Caspian Tern											X		
Forster's Tern									X	X	X	X	
Black Tern									X	X	X	X	
Rock Dove									X	X	X	X	
Band-tailed Pigeon					X	X			X	X	X		
White-winged Dove						X	X	X	X				
Mourning Dove					X	X	X	X	X	X	X	X	X
Anna's Dove						X	X						
Common Ground-Dove						X	X		X				
Black-billed Cuckoo											X		
Yellow-billed Cuckoo					X	X	X	X	X		X		
Greater Roadrunner						X	X	X	X	X			
Common Barn-owl					X	X	X	X	X	X	X		

(Continued)

Table 5—Birds occurring in southwestern and western nonforest habitats—continued

Bird Species	Great Basin shrubsteppe	Sonoran Desert scrub	Chihuahuan Desert scrub	Mojave Desert scrub	Desert riparian deciduous woodlands, marshes	Annual grasslands, farms	River, riparian woodlands, subalpine marshes	Mountain and alpine meadows	Relict conifer forests, madrean evergreen woodlands
Flamulated Owl	X				X		X		
Eastern Screech-Owl			X				X		
Western Screech-Owl	X	X	X	X	X	X	X		
Whiskered Screech-Owl		X			X				
Great Horned Owl	X	X	X	X	X	X	X	X	
Northern Pygmy-Owl	X				X		X	X	
Ferruginous Pygmy-Owl		X			X				
Elf Owl		X	X		X				
Burrowing Owl	X		X	X		X		X	
Spotted Owl	X				X		X		
Great Gray Owl							X		
Long-eared Owl	X	X	X	X	X	X	X	X	
Short-eared Owl	X	X	X	X	X	X	X	X	
Northern Saw-whet Owl	X	X	X	X	X		X	X	
Lesser Nighthawk		X	X	X		X			
Common Nighthawk	X	X	X	X	X	X	X	X	
Common Poorwill	X	X	X	X	X	X	X		
Whip-poor-will		X			X				
Black Swift				X			X	X	
Vaux's Swift							X	X	
White-throated Swift	X	X	X	X	X		X	X	
Broad-billed Hummingbird		X	X		X				
Violet-crowned Hummingbird		X							
Blue-throated Hummingbird		X	X		X				
Magnificent Hummingbird		X			X				
Black-chinned Hummingbird	X	X		X	X		X	X	X
Anna's Hummingbird							X		
Costa's Hummingbird		X		X					
Calliope Hummingbird	X						X	X	
Broad-tailed Hummingbird	X	X					X	X	
Rufous Hummingbird	X	X					X	X	X
Allen's Hummingbird		X					X	X	
Elegant Trogon					X		X		
Belted Kingfisher					X		X		
Lewis' Woodpecker							X		
Acorn Woodpecker		X			X		X		
Gila Woodpecker		X			X				
Red-naped Sapsucker					X				
Yellow-bellied Sapsucker					X		X		
Red-breasted Sapsucker							X		

(Continued)

Table 5—Birds occurring in southwestern and western nonforest habitats—continued

Bird Species	Great Basin shrubsteppe	Sonoran Desert scrub	Chihuahuan Desert scrub	Mojave Desert scrub	Desert riparian deciduous woodlands, marshes	Annual grasslands, farms	River, riparian woodlands, subalpine marshes	Mountain and alpine meadows	Relict conifer forests, madrean evergreen woodlands
Williamson's Sapsucker	X				X		X		
Ladder-backed Woodpecker		X	X	X	X		X		
Nuttall's Woodpecker							X		
Downy Woodpecker					X		X		
Hairy Woodpecker					X		X		
Strickland's Woodpecker		X			X				
Northern Flicker	X	X	X	X	X		X	X	
Pileated Woodpecker							X		
Northern Beardless-Tyrannulet		X			X				
Olive-sided Flycatcher							X		X
Greater Pewee		X			X				
Western Wood-Pewee					X		X		
Willow Flycatcher	X				X		X	X	
Hammond's Flycatcher							X		X
Dusky Flycatcher	X						X	X	
Gray Flycatcher	X								
Western Flycatcher							X	X	
Buff-breasted Flycatcher		X			X				
Black Phoebe		X	X	X	X	X			
Say's Phoebe	X	X	X	X		X	X		
Vermilion Flycatcher		X	X		X				
Dusky-capped Flycatcher		X			X				
Ash-throated Flycatcher		X	X	X	X		X		X
Brown-crested Flycatcher		X			X		X		
Sulphur-bellied Flycatcher		X			X				
Cassin's Kingbird	X	X	X	X	X	X			
Thick-billed Kingbird		X	X		X				
Western Kingbird	X	X	X	X	X	X	X		
Eastern Kingbird	X		X			X	X		
Rose-throated Becard		X			X				
Horned Lark	X	X	X	X		X	X	X	
Purple Martin		X			X	X	X	X	
Tree Swallow					X	X	X	X	
Violet-green Swallow	X				X	X	X	X	
Northern Rough-winged Swallow	X				X	X	X		
Bank Swallow	X	X			X	X	X		
Cliff Swallow					X	X	X	X	X
Barn Swallow	X	X	X	X	X	X	X		X
Gray Jay							X		
Steller's Jay							X		X

(Continued)

Table 5—Birds occurring in southwestern and western nonforest habitats—continued

Bird Species	Great Basin shrubsteppe	Sonoran Desert scrub	Chihuahuan Desert scrub	Mojave Desert scrub	Desert riparian deciduous woodlands, marshes	Annual grasslands, farms	River, riparian woodlands, subalpine marshes	Mountain and alpine meadows	Relict conifer forests, madrean evergreen
Scrub Jay	X	X		X		X	X		X
Gray-breasted Jay			X		X				
Pinyon Jay	X	X	X	X			X		
Clark's Nutcracker							X	X	X
Black-billed Magpie	X				X	X	X	X	
Yellow-billed Magpie						X	X		
American Crow	X	X	X	X	X	X	X	X	
Chihuahuan Raven		X	X			X			
Common Raven	X	X	X	X	X	X	X	X	X
Black-capped Chickadee	X						X	X	
Mountain Chickadee	X						X	X	
Chestnut-backed Chickadee							X		
Bridled Titmouse		X			X		X		
Plain Titmouse	X	X	X		X		X		
Verdin		X	X	X					
Bushtit	X	X			X		X		
Red-breasted Nuthatch							X		
White-breasted Nuthatch					X		X		
Pygmy Nuthatch					X		X		
Brown Creeper					X		X		
Cactus Wren		X	X	X					
Rock Wren	X	X	X	X					
Canyon Wren	X	X	X	X			X		
Bewick's Wren		X	X	X		X	X		X
House Wren	X	X	X		X	X	X	X	
Winter Wren					X		X		
Marsh Wren	X				X		X	X	
American Dipper							X	X	
Golden-crowned Kinglet							X		
Ruby-crowned Kinglet					X		X		
Blue-gray Gnatcatcher	X	X	X		X		X		
Black-tailed Gnatcatcher		X	X		X				
Western Bluebird	X				X	X	X	X	
Mountain Bluebird	X	X	X	X		X	X	X	
Townsend's Solitaire	X				X		X	X	
Veery							X		
Swainson's Thrush					X		X		
Hermit Thrush	X					X	X	X	
American Robin	X	X	X	X	X	X	X	X	
Varied Thrush							X	X	

(Continued)

Table 5—Birds occurring in southwestern and western nonforest habitats—continued

Bird Species	Great Basin shrubsteppe	Sonoran Desert scrub	Chihuahuan Desert scrub	Mojave Desert scrub	Desert riparian deciduous woodlands, marshes	Annual grasslands, farms	River, riparian woodlands, subalpine marshes	Mountain and alpine meadows	Relict conifer forests, madrean evergreen woodlands
Wrentit							X		
Gray Catbird							X		
Northern Mockingbird	X	X	X	X	X	X	X		
Sage Thrasher	X	X		X		X	X		
Bendire's Thrasher		X	X		X	X			
Curve-billed Thrasher		X	X		X				
California Thrasher							X		
Crissal Thrasher					X				
Le Conte's Thrasher	X			X					
Water Pipit	X					X	X	X	
Bohemian Waxwing	X						X		
Cedar Waxwing	X	X	X	X	X	X	X		
Phainopepla		X	X		X				
Northern Shrike	X					X	X	X	
Loggerhead Shrike	X	X	X	X	X	X	X	X	
European Starling	X	X	X	X	X	X	X	X	X
Bell's Vireo				X	X	X			
Gray Vireo	X								
Solitary Vireo	X				X		X		X
Hutton's Vireo		X			X		X		
Warbling Vireo					X		X		
Orange-crowned Warbler	X				X		X		
Nashville Warbler							X		
Virginia's Warbler	X				X		X		
Lucy's Warbler		X	X	X	X		X		
Yellow Warbler	X				X		X	X	
Yellow-rumped Warbler	X				X		X		
Black-throated Gray Warbler	X	X		X	X		X		X
Townsend's Warbler							X		
Hermit Warbler							X		
Grace's Warbler							X		
Ovenbird							X		
MacGillivray's Warbler	X						X	X	
Common Yellowthroat					X		X	X	
Wilson's Warbler					X		X	X	
Red-faced Warbler					X		X		
Painted Redstart					X		X		
Yellow-breasted Chat	X				X		X		
Olive Warbler							X		
Hepatic Tanager							X		

(Continued)

Table 5—Birds occurring in southwestern and western nonforest habitats—continued

Bird Species	Great Basin shrubsteppe	Sonoran Desert scrub	Chihuahuan Desert scrub	Mojave Desert scrub	Desert riparian deciduous woodlands, marshes	Annual grasslands, farms	River, riparian woodlands, subalpine marshes	Mountain and alpine meadows	Relict conifer forests, madrean evergreen woodlands
Summer Tanager					X		X		
Western Tanager	X				X		X		
Northern Cardinal		X	X		X				
Pyrrhuloxia		X	X		X				
Rose-breasted Grosbeak							X		
Black-headed Grosbeak	X				X		X		X
Blue Grosbeak					X	X	X		
Lazuli Bunting	X	X			X	X	X	X	
Indigo Bunting					X		X		
Varied Bunting		X	X		X				
Green-tailed Towhee	X	X			X		X		
Rufous-sided Towhee	X	X			X		X		X
Brown Towhee		X	X	X	X	X	X		
Abert's Towhee		X	X		X				
Botteri's Sparrow		X							
Cassin's Sparrow		X	X			X			
Rufous-winged Sparrow		X							
Rufous-crowned Sparrow	X	X	X				X		
American Tree Sparrow	X						X		
Chipping Sparrow	X	X	X	X	X	X	X	X	
Clay-colored Sparrow		X	X			X			
Brewer's Sparrow	X	X	X	X	X	X			
Black-chinned Sparrow	X	X	X						X
Vesper Sparrow	X	X	X	X	X	X	X	X	
Lark Sparrow	X	X				X	X		
Black-throated Sparrow	X	X	X	X	X				
Sage Sparrow	X	X	X	X			X		
Lark Bunting						X			
Savannah Sparrow	X	X	X		X	X	X	X	
Grasshopper Sparrow		X	X	X	X	X	X		
Fox Sparrow	X				X		X		
Song Sparrow	X	X	X	X	X	X	X	X	
Lincoln's Sparrow					X		X	X	
Swamp Sparrow							X	X	
White-throated Sparrow			X		X		X		
Golden-crowned Sparrow						X	X	X	
White-crowned Sparrow	X	X	X	X	X	X	X	X	
Harris' Sparrow	X						X		
Dark-eyed Junco	X	X	X	X	X	X	X	X	
Yellow-eyed Junco		X			X				

(Continued)

Table 5—Birds occurring in southwestern and western nonforest habitats—continued

Bird Species	Great Basin shrubsteppe	Sonoran Desert scrub	Chihuahuan Desert scrub	Mojave Desert scrub	Desert riparian deciduous woodlands, marshes	Annual grasslands, farms	River, riparian woodlands, subalpine marshes	Mountain and alpine meadows	Relict conifer forests, madrean evergreen woodlands
McCown's Longspur		X	X			X		X	
Upland Longspur	X					X		X	
Chestnut-collared Longspur		X	X			X	X		
Bobolink							X		
Red-winged Blackbird					X	X	X	X	
Tricolored Blackbird						X	X		
Eastern Meadowlark		X	X						
Western Meadowlark	X	X	X	X	X	X	X	X	
Yellow-headed Blackbird					X		X		
Rusty Blackbird							X		
Brewer's Blackbird					X	X	X	X	
Great-tailed Grackle		X	X		X	X			
Common Grackle							X		
Bronzed Cowbird		X			X				
Brown-headed Cowbird	X	X	X	X	X	X	X	X	
Hooded Oriole		X			X				
Northern Oriole					X	X	X		
Scott's Oriole		X	X	X					X
Rosy Finch	X					X		X	
Pine Grosbeak	X						X	X	
Purple Finch	X	X			X		X	X	
Cassin's Finch	X						X	X	
House Finch	X	X			X	X	X	X	
Red Crossbill	X						X		
Common Redpoll	X						X		
Pine Siskin	X					X	X	X	
Lesser Goldfinch	X	X	X	X	X	X			
Lawrence's Goldfinch		X		X		X			
American Goldfinch	X				X	X	X	X	
Evening Grosbeak	X				X		X		
House Sparrow	X	X	X	X	X	X	X	X	

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Red-tailed Hawk	<i>Buteo jamaicensis</i>	89
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Black-capped Vireo	<i>Vireo atricapillus</i>	377
Gray Vireo	<i>Vireo vicinior</i>	378
Solitary Vireo	<i>Vireo solitarius</i>	379
Yellow-throated Vireo	<i>Vireo flavifrons</i>	380
Hutton's Vireo	<i>Vireo huttoni</i>	381
Warbling Vireo	<i>Vireo gilvus</i>	382

Philadelphia Vireo	<i>Vireo philadelphicus</i>	383
Red-eyed Vireo	<i>Vireo olivaceus</i>	384
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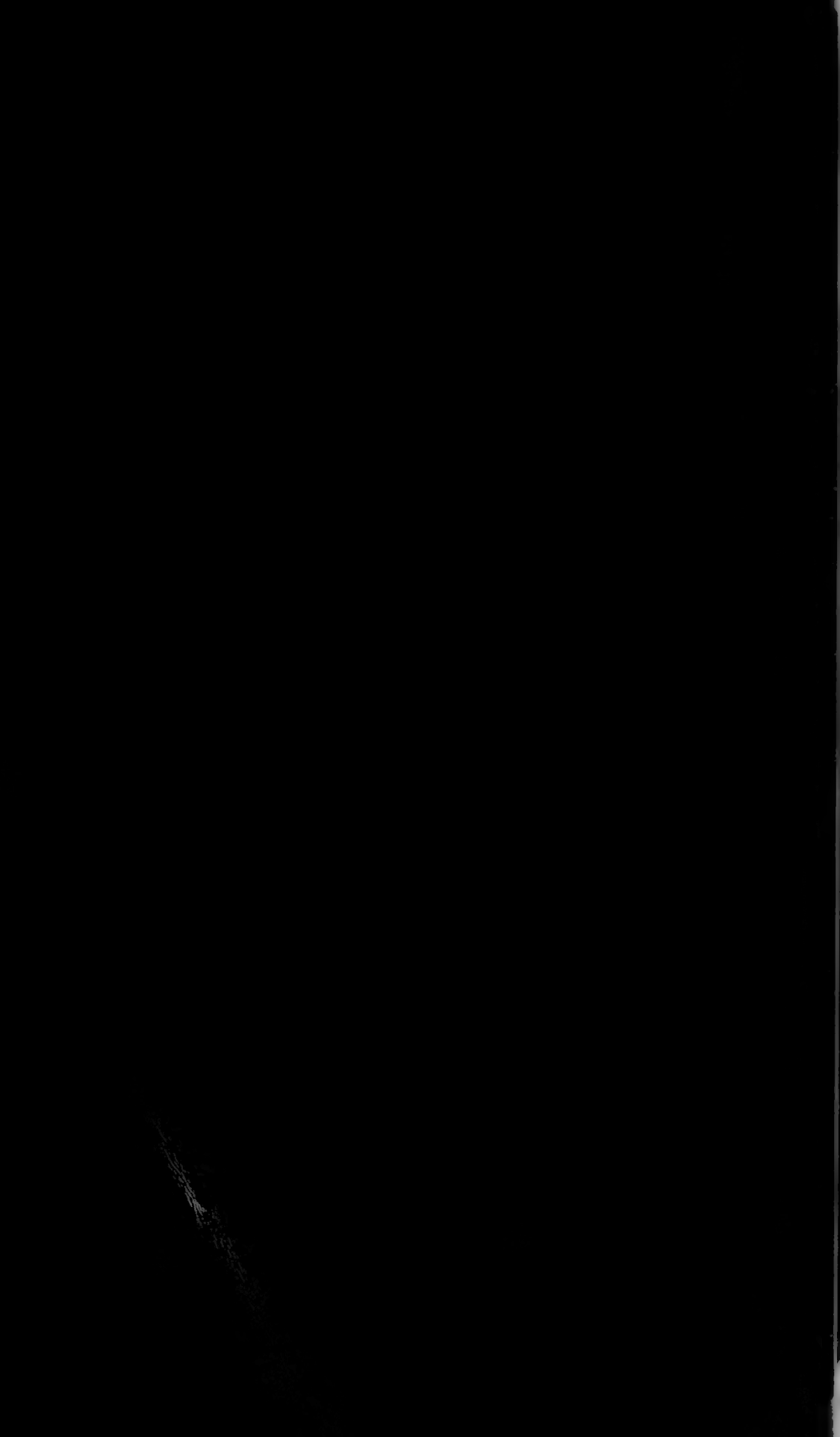
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Economic Picture of U.S. Agriculture

Assistant Secretary of Agriculture for Economics summarizes key points in the 1990 agricultural outlook:

U.S. agriculture became more reliant on foreign markets in the 1970's and 1980's, and events that, more than any others, caused the U.S. farm problems of the 1980's were related to the world economy.

U.S. agriculture has regained its world competitiveness. The U.S. share of world grain trade is now back to near 50 percent compared with 35 percent in 1985. Total U.S. agricultural exports for FY 1989 were nearly \$40 billion, over 50 percent higher than FY 1986. A drop of nearly a fourth in the value of the dollar and an upturn in global economic growth helped spur this export turnaround. Although slowing, U.S. economic growth is expected to be about 2.5 percent in 1990, the eighth consecutive annual expansion.

Increased consumption and output reduction due to drought raised overall farm prices to a record high in 1989. Farm prices will likely fall about 3-4 percent in 1990 as production of major crops increases.

With another strong income year, farmers' balance sheets should continue to improve in 1990. Farm assets are expected to increase about 4 percent, while debt rises only slightly above last year's level.

U.S. crop production in 1990 will likely rise and prices fall for some major crops. However, larger crop marketings are expected to more than offset any price declines. With crop receipts expected to be record high, livestock receipts near last year's record, and overall production expenses holding steady, 1990 cash farm income should be near the record 1988 level. Farmers' overall financial position should also improve as their debt-to-asset ratio continues to decline.

--From a statement by the Assistant Secretary of
Agriculture for Economics, February 22, 1990

The following charts, based on the Assistant Secretary's February statement, present an overview of the current health of American agriculture. The charts move from the national and international arenas to farm economic health measures, crop and livestock production, and food prices.

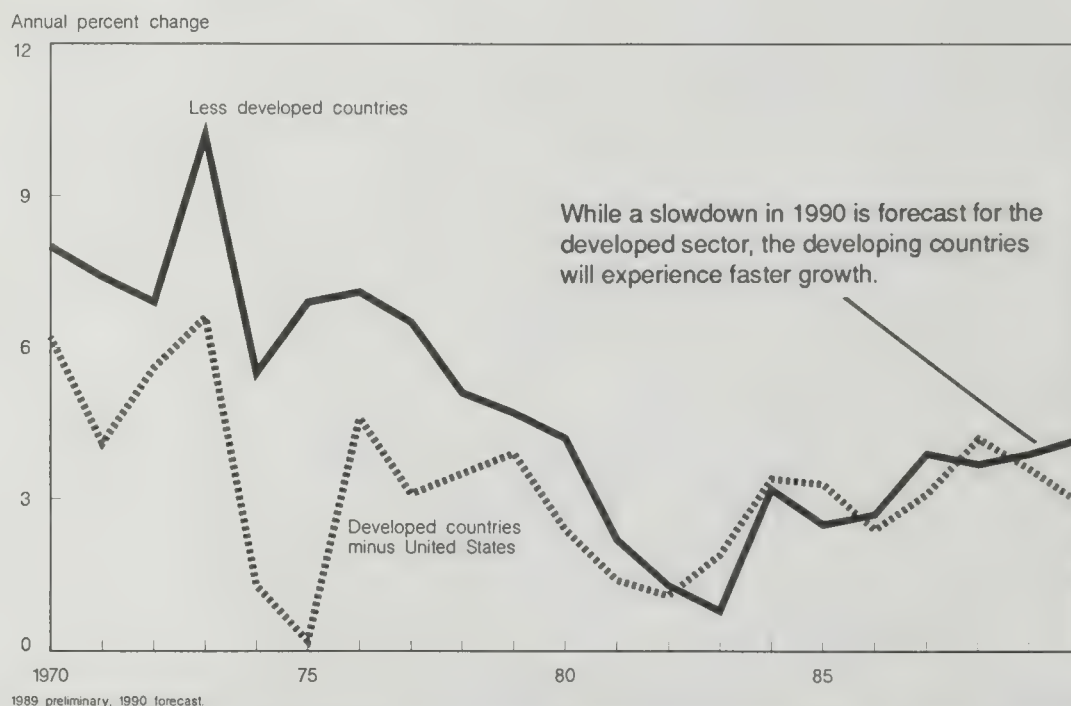
International and National Economic Outlook

World inflation is expected to slow this year, mostly due to some easing of inflation in the developed countries. U.S. inflation is likely to be a moderate 3.5-4 percent. U.S. economic growth is projected to be about 2.5 percent in 1990. Spending on new plants and equipment and rising exports are expected to contribute most to GNP increases.

T1

Economic growth abroad strongest in less developed countries

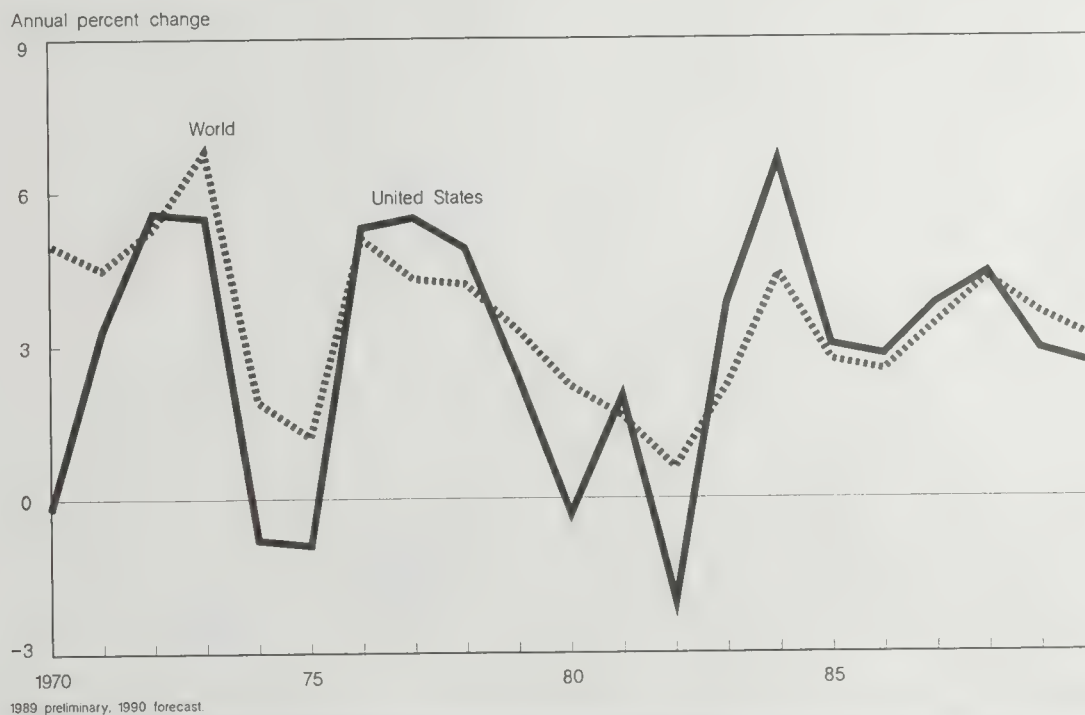
World economic growth averaged 2.9 percent per year in the 1980's. Developed countries grew 2.8 percent, less developed countries 3.4 percent. The world's fastest growing region is the Pacific Basin, led by South Korea, Taiwan, Hong Kong, and Singapore.



T2

World and U.S. economic growth continue to expand

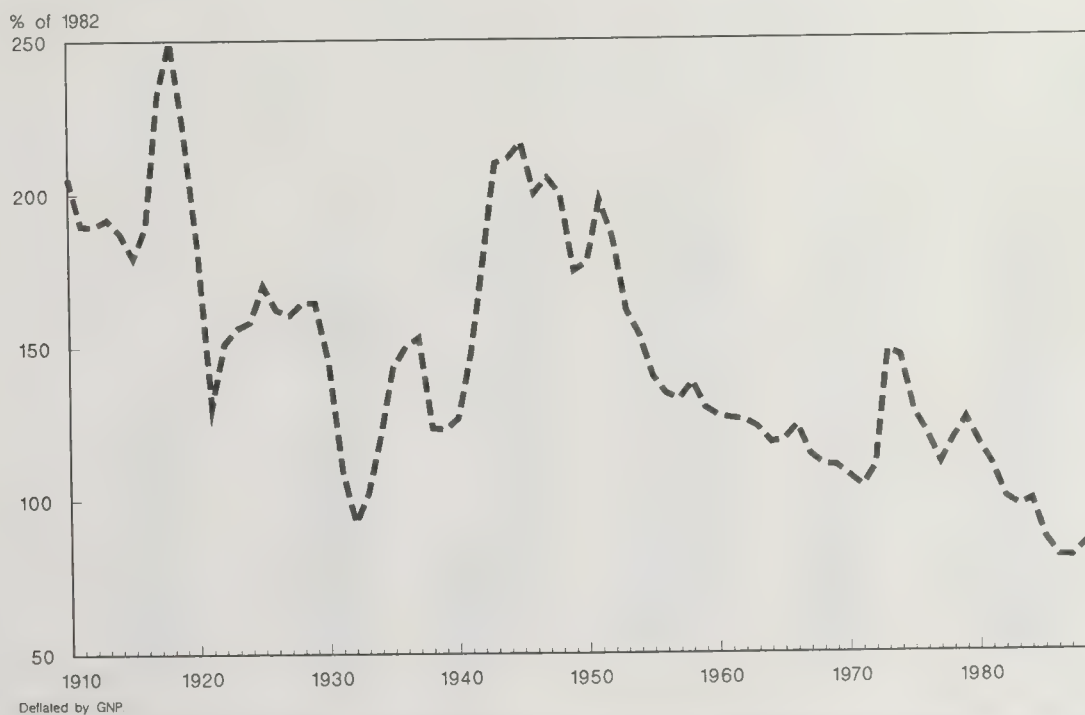
World economic expansion is forecast at 3.1 percent with U.S. growth at 2.5 percent. Foreign growth in excess of U.S. growth and modest currency movements will combine to produce a slight improvement in real net U.S. exports in 1990.



T3

Prices received by farmers experience considerable year-to-year variation

Prices received by U.S. farmers have been trending downward since 1910 although prices have risen moderately during the past couple of years, reflecting tighter crop supplies and expanding world trade.



Farm Financial Conditions

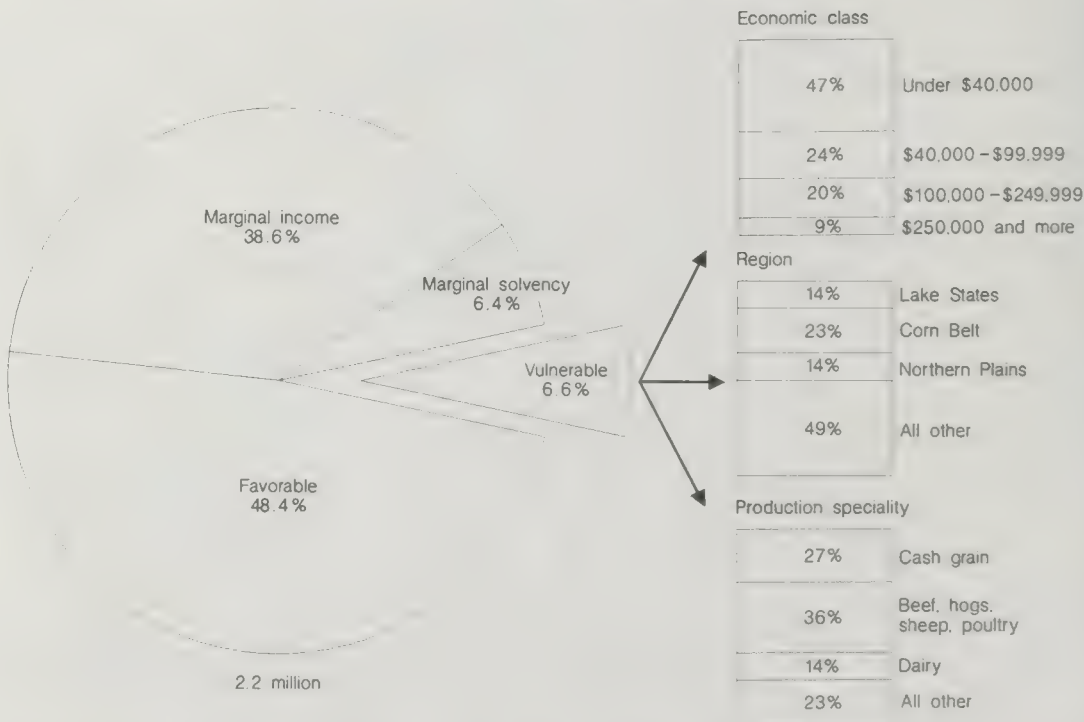
The farm financial picture is favorable. Farmers' cash receipts will reach a record high and farm production costs are likely to be stable. Net cash income in 1990 is expected to reach more than \$50 billion for the fifth consecutive year, exceeding 1989 by 2-4 percent. While farm debt may increase slightly (ending a 6-year trend of debt retirement), rising land values will enhance farmers' assets, improving their equity position by 4-5 percent. Government payments will decline with smaller disaster payments.

T4

Percent of farm operator households in stress remains at low level

The share of farm operator households classified as financially vulnerable, as of January 1, 1989, remained near 1988 levels, which had fallen 30 percent from the previous year.

- Favorable—**
Positive net income and low debt load.
- Marginal income—**
Negative net income and low debt load.
- Marginal solvency—**
Positive net income and high debt load.
- Vulnerable—**
Negative net income and high debt load

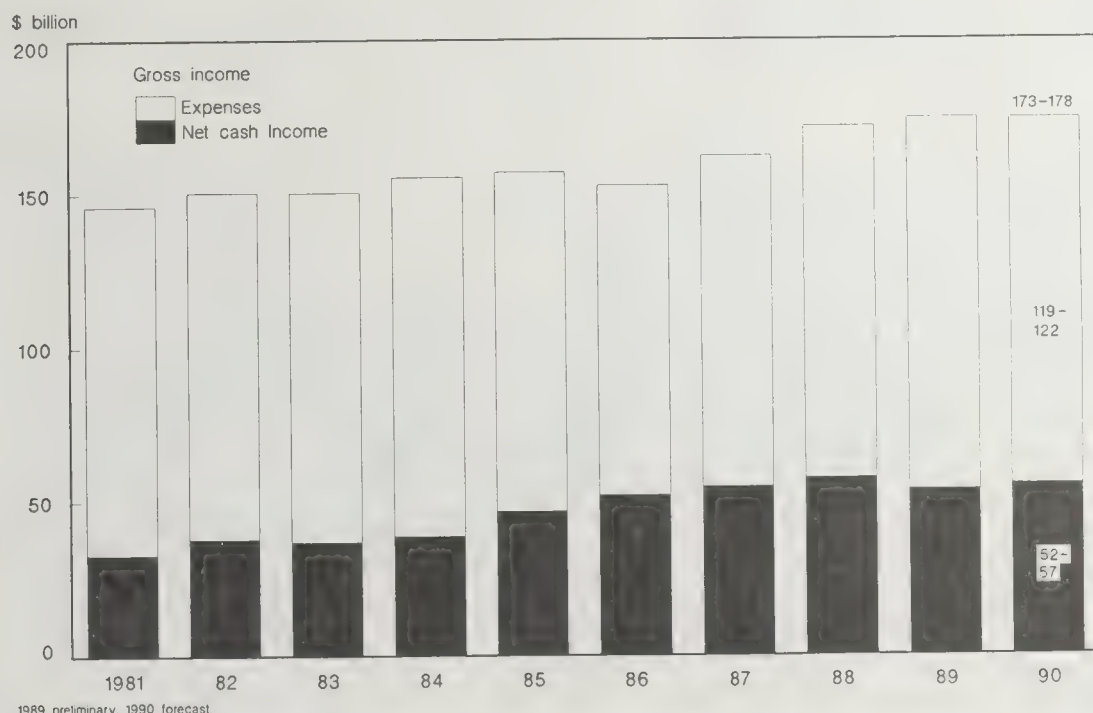


Source: Federal Costs and Returns Survey household stress rates applied to the Agricultural Statistics Board, NASS, estimate of farm numbers by economic class.

T5

Cash farm income increases

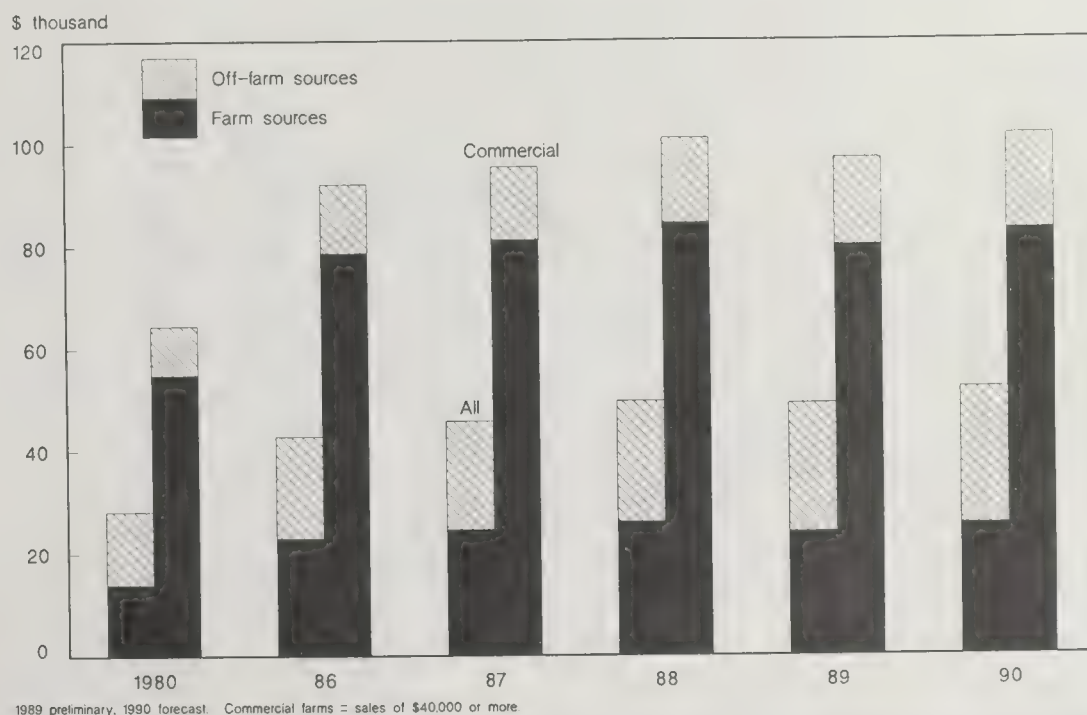
Higher crop receipts from \$2-\$5 billion will push cash income up 2-4 percent to the mid-\$50 billion range. Net cash income has been above \$50 billion for 5 years in a row.



T6

Income per farm supplemented by off-farm sources

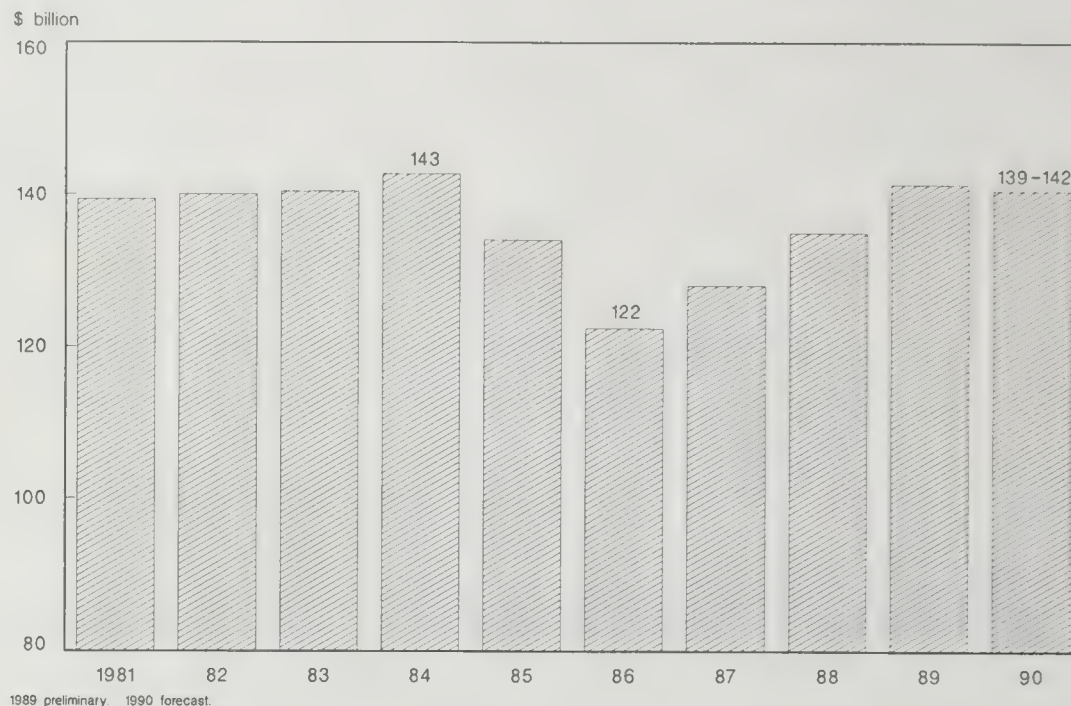
Income from off-farm sources will continue to constitute over 50 percent of average per farm income. Off-farm income will be less than 20 percent of income for commercial farms (\$40,000 or more of annual sales).



T7

Farm production costs remain stable

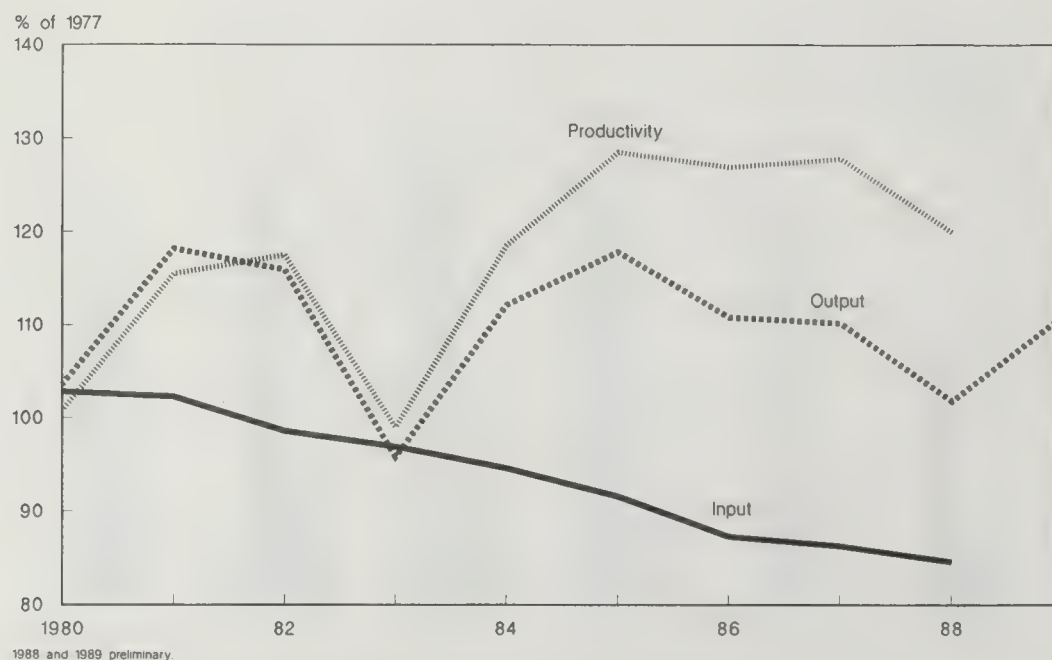
A 15-percent expected decline in feed costs will offset 2-4 percent increases in fertilizer, fuels, repairs, and depreciation. Total production costs should remain stable at around \$141 billion.



T8

Farm output, input, and productivity influenced by drought

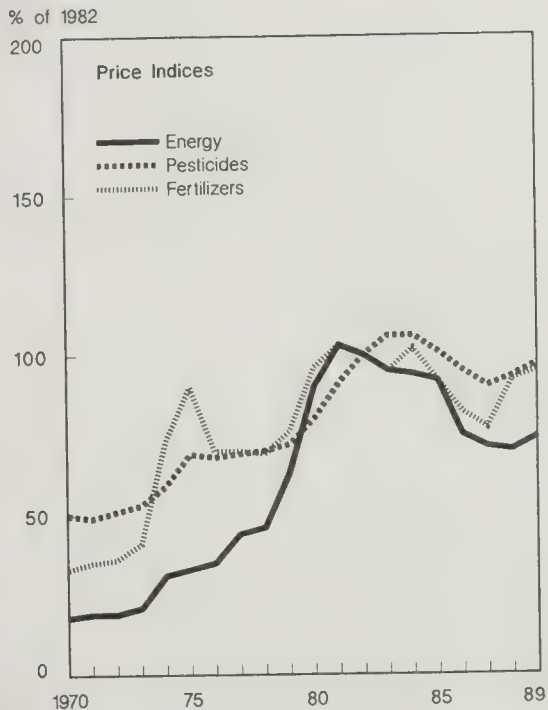
Farm output did not change much during the 1980's, except in years of major drought (1983, 1988). Farmers were able to maintain their output even with a steady decline in use of inputs, because of generally increasing levels of productivity.



T9

Costs of farm inputs rise

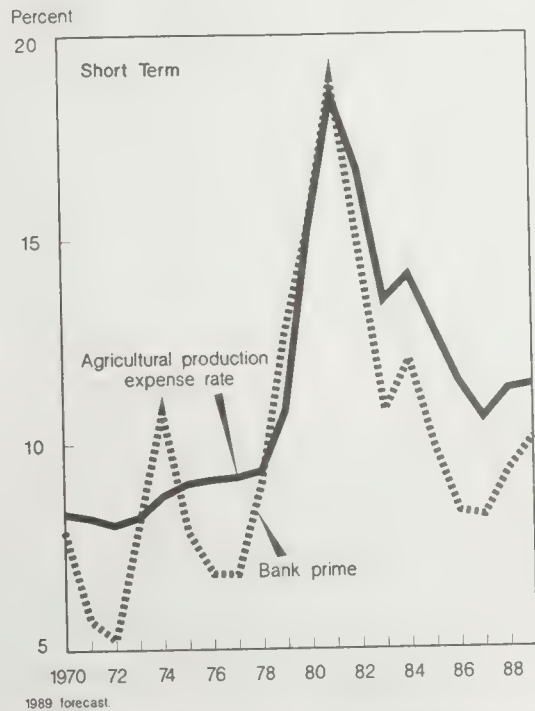
Fertilizer, pesticides, and energy expenses increased in 1989 due to higher prices and higher per acre use.



T10

Agricultural interest rates hold steady

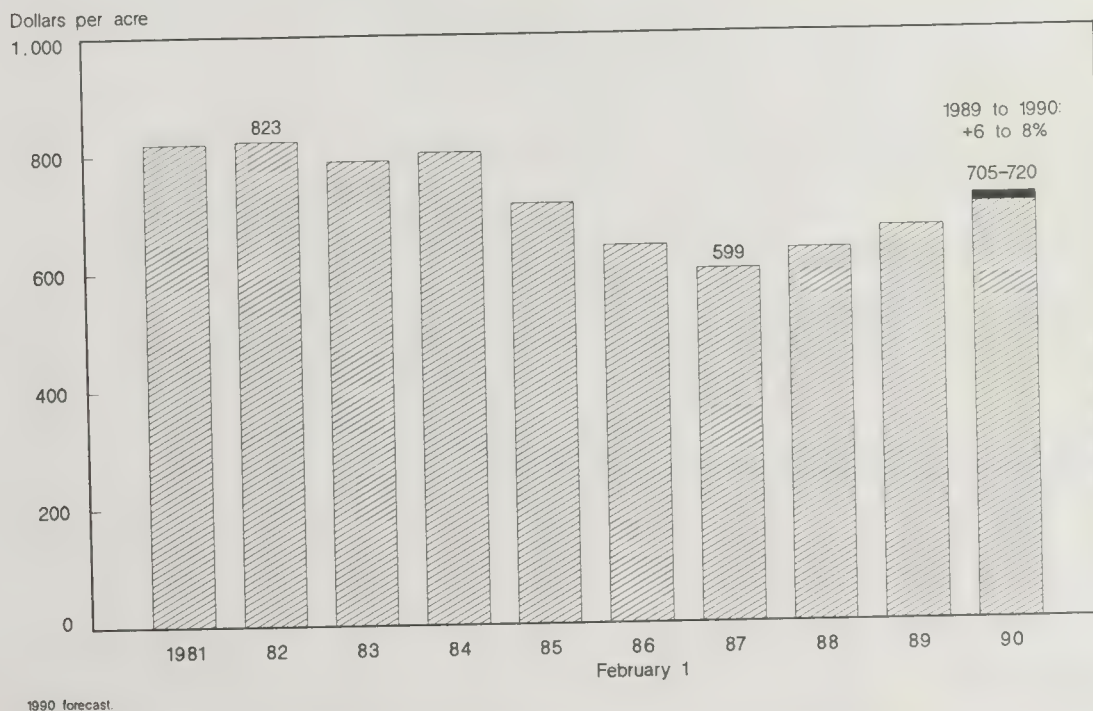
Interest expense remained stable for a fourth year, illustrating farmers' more conservative approach to financing.



T11

Rising farm real estate values improve farm assets

Farm assets will likely increase due to an expected 6-8 percent increase in land values.



T12

Assets, debt, and equity show improving balance sheets for farmers

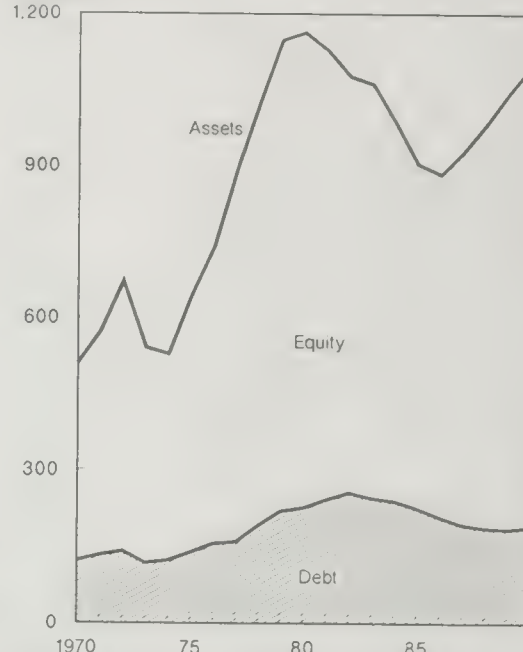
Farm assets and equity are expected to increase about 5 percent in 1990, while debt per farm may increase only slightly.

Per Farm
\$ thousand
1,200



1989 preliminary, 1990 forecast.

Per Commercial Farm
\$ thousand
1,200



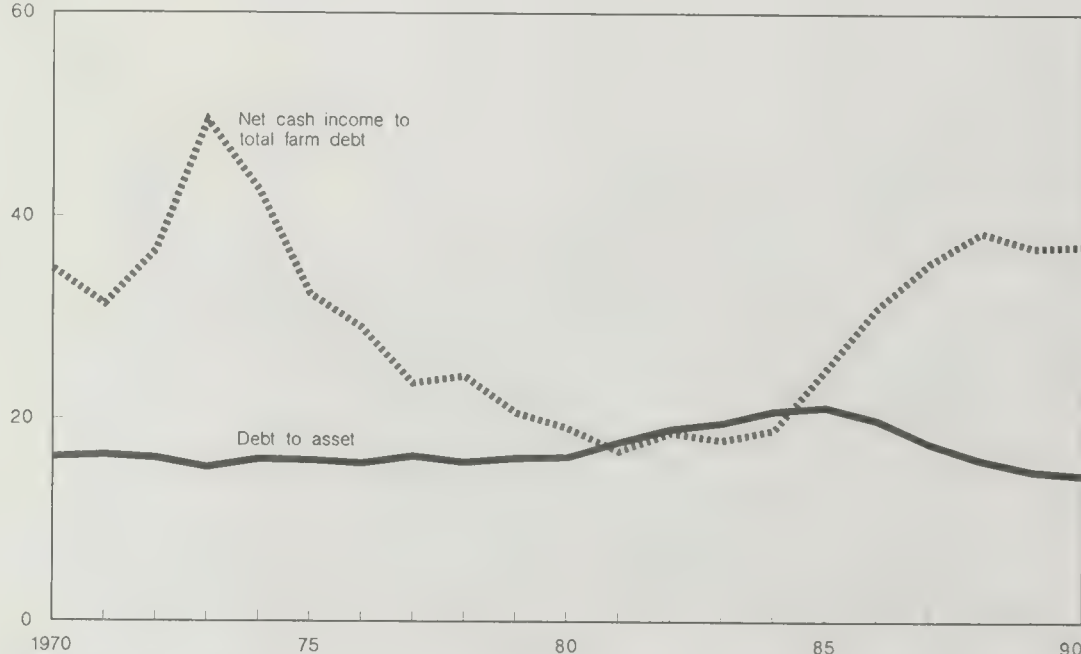
1989 preliminary, 1990 forecast. Commercial farms=sales of \$40,000 or more

T13

Selected financial ratios are favorable for farming

The debt-to-asset ratio may decline slightly in 1990 for the fifth year in a row. The net cash income-to-debt ratio is expected to remain stable.

Ratio
60

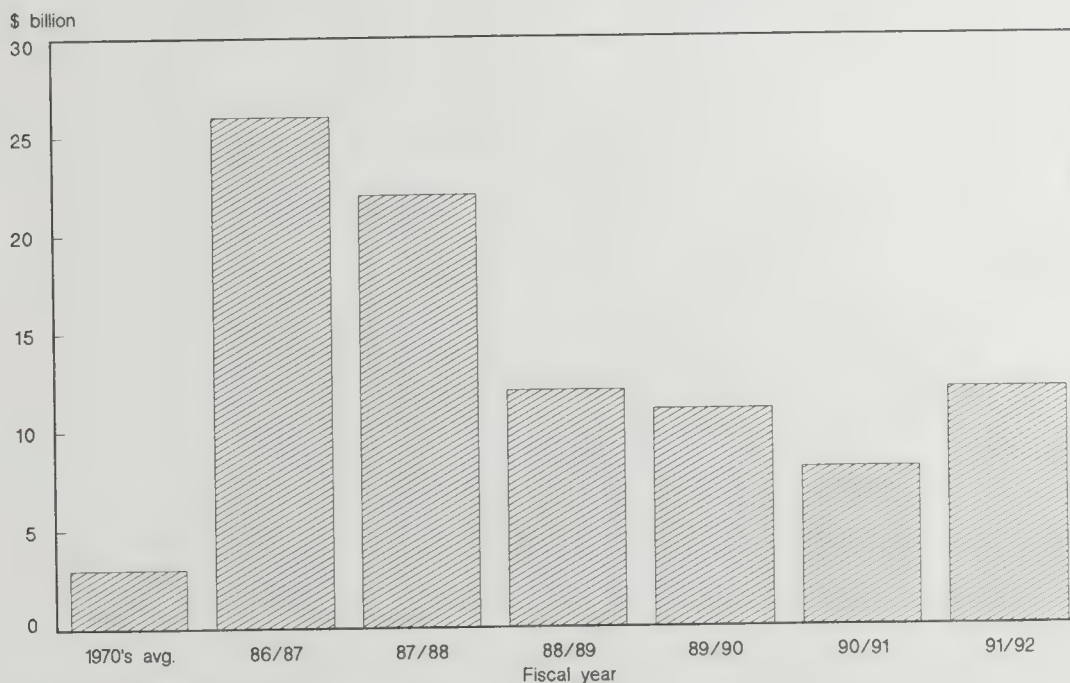


1989 preliminary, 1990 forecast

T14

Farm program outlays fluctuate

Net outlays for U.S. farm programs in fiscal 1990 are expected to drop because of smaller disaster payments. But current law calls for FY 1990 total outlays to rise by over \$3 billion, due mainly to increased direct cash outlays.



1990/91 preliminary, 1991/92 forecast.

Net outlays for U.S. farm programs

Item	1986/87	1987/88	1988/89	1989/90	1990/91 ^P	1991/92 ^F
<i>Billion dollars</i>						
Direct cash outlays	6.2	5.2	4.0	5.8	4.5	8.4
Net lending activity ¹	11.9	12.2	-4.6	-2.3	-. ²	1.4
CCC dairy purchase	2.2	1.2	.6	.4	.5	.5
All other	5.5	3.8	12.4	6.6	3.2	1.4
Total	25.8	22.4	12.4	10.5	8.2	11.7

¹ Commodity loans less payments. ² Less than \$50 million. P=Preliminary. F=Forecast.

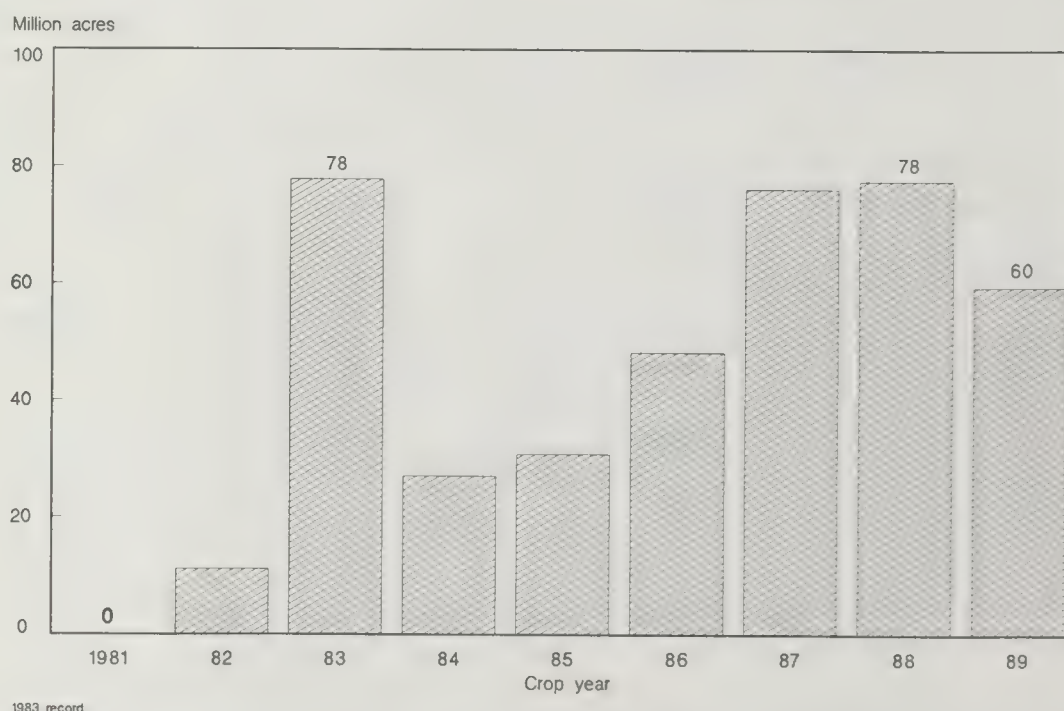
Crop Production

Global and U.S. crop production in 1989/90 rebounded from the weather-reduced levels of the previous season. Acreage reduction programs (ARP's) for wheat, cotton, and rice have been reduced for the 1990 crops, while the ARP for feed grains is unchanged. Grain production is forecast up more than 7 percent. Wheat, coarse grain, and rice output are all larger. Oilseed production is up, while cotton production is declining. Although world and U.S. harvests of most crops were larger this season, use will exceed production, cutting further into ending stocks.

T15

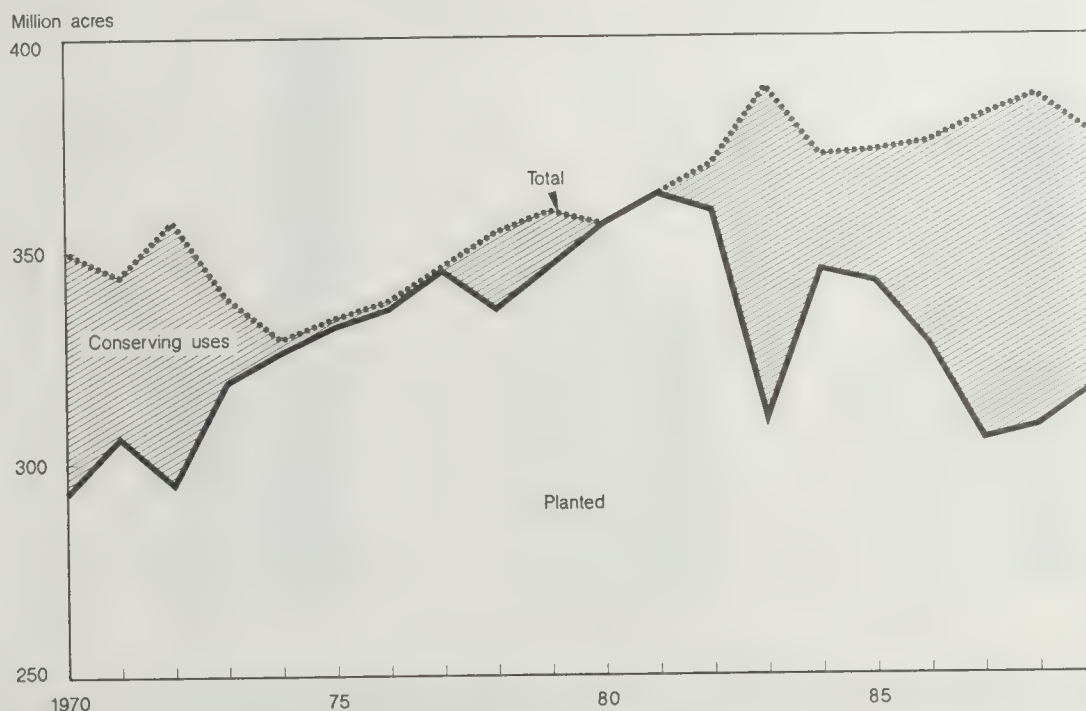
Amount of acreage idled under Federal programs has dropped

About 60 million acres were idled under Federal programs in 1989, well below the record of nearly 78 million in 1983 and 1988.



U.S. crop acreage planted increases: Less acreage placed in conserving uses

Although less land was idled under annual programs, long-term Conservation Reserve Program enrollment grew to nearly 30 million acres, making up half of the total acreage idled for conservation in 1989. Acreage planted in 1989 increased 12 million acres above the reduced level of 1987. With smaller set-asides for wheat, cotton, and rice, planting of major crops is expected to increase in 1990.



U.S. crop acreage planted, harvested, and placed in conserving uses

Item	1984	1985	1986	1987	1988	1989
Million acres						
Principal crops:						
Feed grains	122.1	128.1	119.8	106.8	101.8	106.2
Wheat	79.2	75.6	72.1	65.8	65.5	76.6
Soybeans	67.8	63.1	60.4	58.2	58.8	60.7
Cotton	11.1	10.7	10.0	10.4	12.5	10.6
Rice	2.8	2.5	2.4	2.4	2.9	2.7
Other crops	NA	62.2	62.6	61.3	66.7	60.4
Total planted crops ¹	345.1	342.2	327.3	304.9	308.2	317.2
Total harvested crops ¹	335.7	330.9	311.2	289.4	289.8	305.6
Conservation programs:						
ARP	17.7	21.9	36.3	44.6	40.2	18.5
PLD	5.7	8.8	6.4	8.9	4.1	NA
PIK	3.6	NA	NA	NA	NA	NA
0/92-50/92	NA	NA	3.5	7.0	8.8	11.4
Long-term CRP	NA	NA	2.0	15.7	24.5	29.6
Total conserving uses	27.0	30.7	48.2	76.2	77.6	59.5

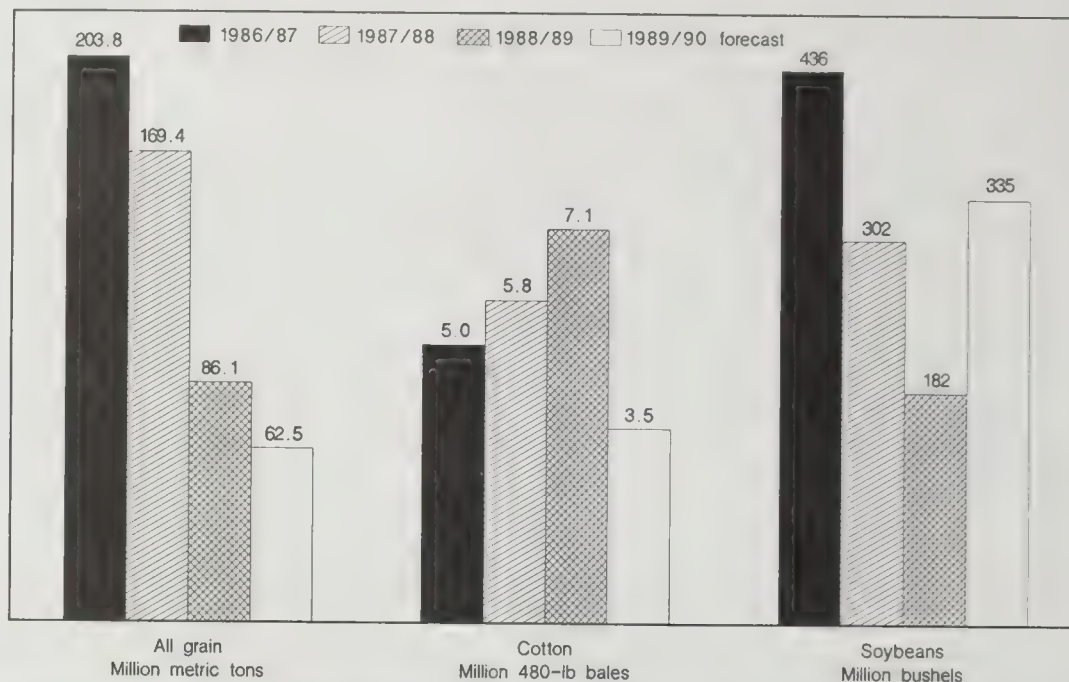
NA=Not available. ¹Includes corn, sorghum, oats, barley, wheat, rice, rye, soybeans, flaxseed, peanuts, sunflower, cotton, all hay, dry edible peas and beans, lentils, potatoes, sweetpotatoes, tobacco, sugarcane, and sugar beets. Harvested acreages for winter wheat, rye, all hay, tobacco, and sugarcane are used in computing total planted acreage. Sources: NASS and ASCS, USDA.

T17

End-of-season inventories show wide variations

Projected grain inventories of 62 million tons continue a downward trend, while cotton stocks are dropping to the lowest level since 1983/84. Soybean stocks may about double from last season's low level.

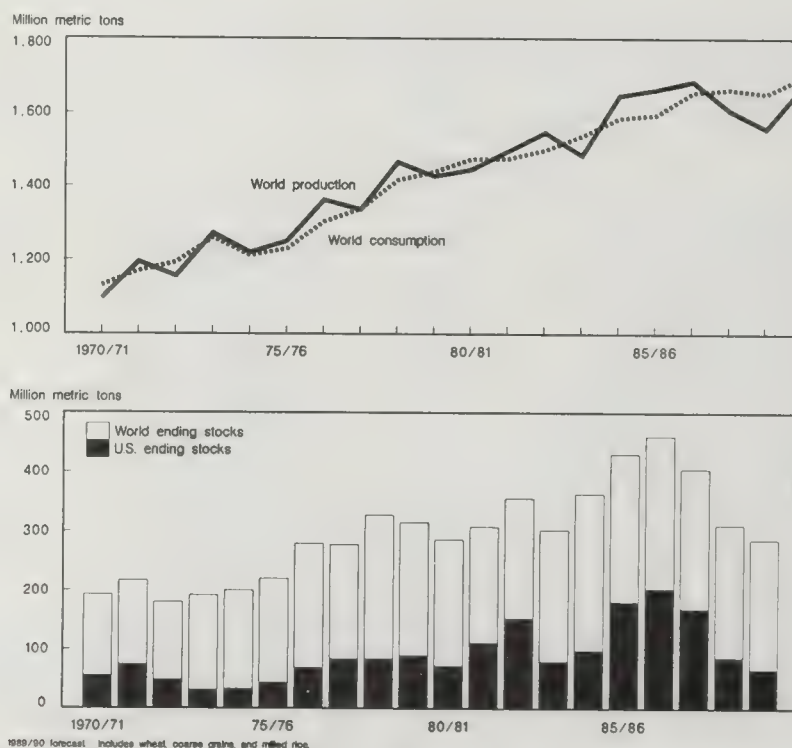
Production units



T18

World grain consumption outweighs production

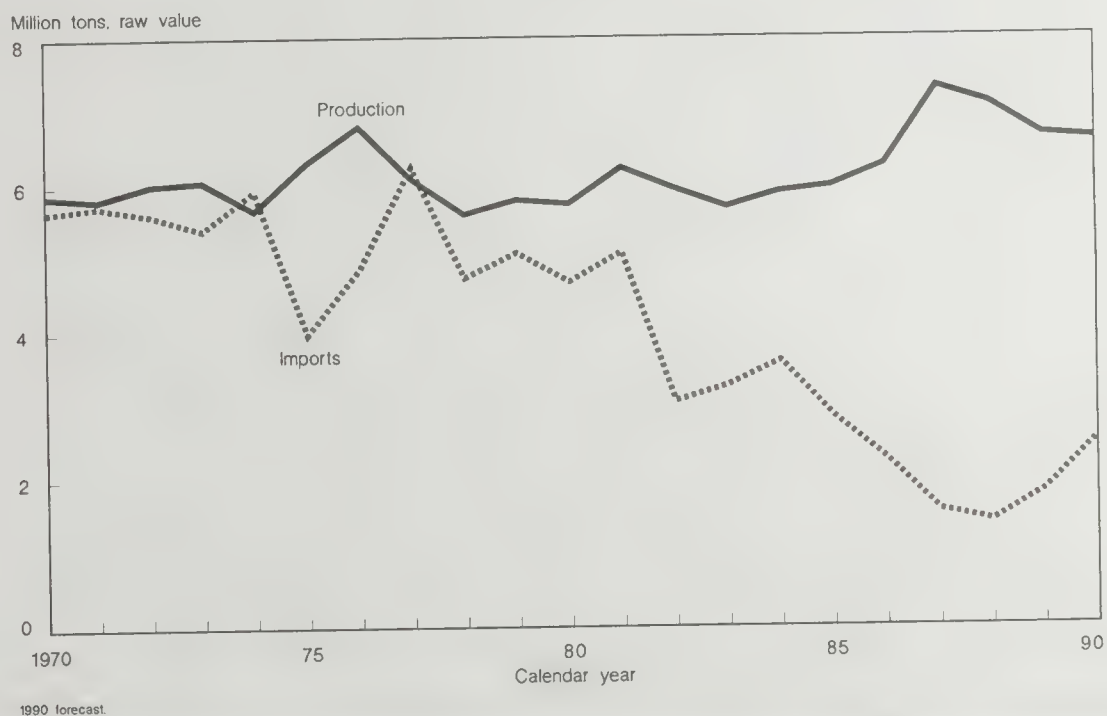
World grain consumption has exceeded production for the past 3 years, leading to another decline in world stocks.



T19

U.S. sugar production declines slightly while imports rise

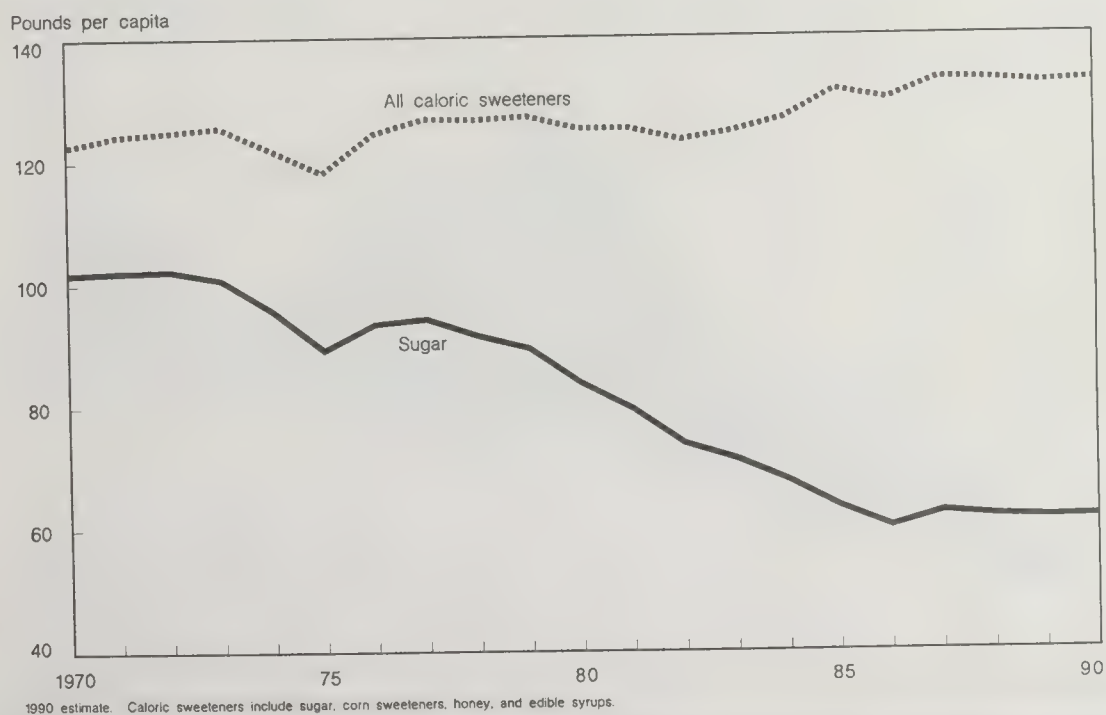
U.S. sugar production is forecast to decline to 6.6 million short tons in 1990, 1 percent below last year's level.



T20

U.S. caloric sweetener consumption is steady

U.S. sugar consumption is expected to remain steady for the fourth straight year, following 10 years of decline as corn sweeteners replaced sugar in soft drinks.



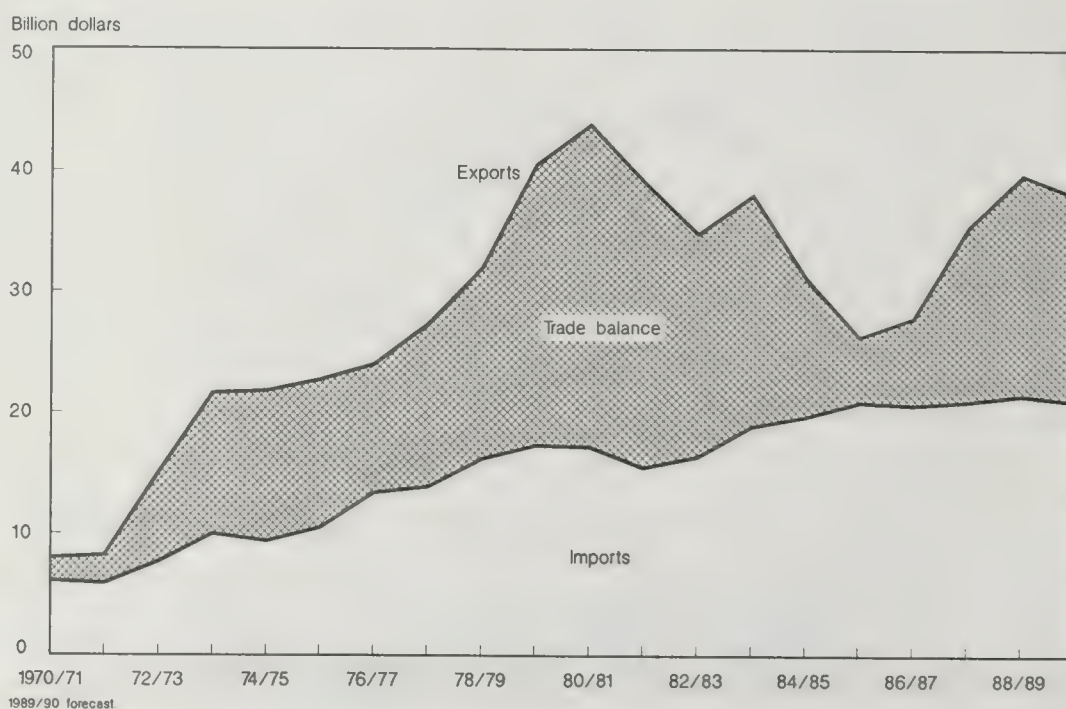
Agricultural Trade

On the basis of the February USDA global supply and demand assessment, the FY 1990 export forecast is slightly smaller than the FY 1989 total. Compared with the 1986 low of 110 million tons, U.S. export volume will be about a third higher in 1990. Similarly, the U.S. share of world trade has returned to near its long-term average of 25 percent.

T21

U.S. agricultural exports show turnaround

U.S. agricultural exports in FY 1990 should total \$38 billion, up 44 percent from 1986. U.S. agricultural imports should hold steady at just over \$21 billion.



T22

U.S. agricultural export volume remains relatively stable

U.S. corn, cotton, and soybean exports are expected to increase in 1990, offsetting an anticipated drop in wheat and soybean meal exports.

Item	1980	1986	1987	1988	1989	1990 ^F
Million tons						
Grains and preparations	116.2	74.4	90.2	108.9	115.0	112.6
Wheat	36.1	25.5	28.2	40.5	37.8	33.0
Corn	61.4	31.1	39.3	44.0	50.6	55.0
Sorghum	8.2	4.1	5.1	6.1	8.1	6.5
Rice	3.0	2.4	2.5	2.2	3.1	2.5
Oilseeds and products	35.6	27.6	29.7	29.7	21.1	22.4
Soybeans and products	32.2	26.2	28.6	28.0	19.5	20.9
Animals and products	2.5	2.6	2.6	2.8	3.3	3.3
Fruits, nuts, and vegetables	3.3	3.4	3.8	4.2	5.0	5.0
Cotton	2.0	.5	1.3	1.4	1.5	1.7
Other	3.9	1.4	1.7	1.3	1.8	.5
Total	163.5	109.9	129.3	148.4	147.8	145.5

Fiscal years, October-September. F=Forecast.

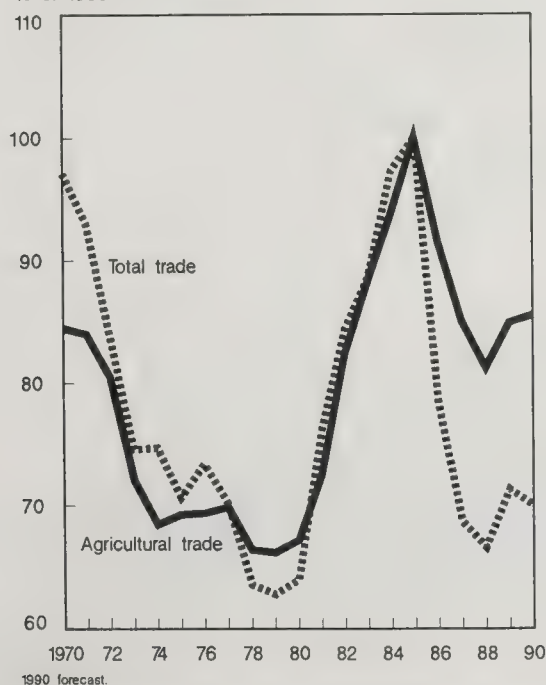
T23

Dollar exchange rates falling

The dollar should depreciate in 1990, which should spur demand for U.S. farm products. However, the dollar will likely appreciate against currencies of our major competitors, such as Brazil and Argentina.

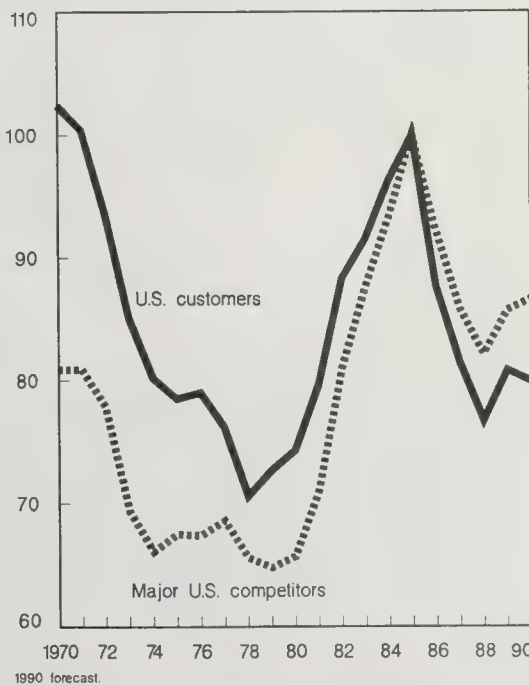
Total Trade vs. Agricultural Trade

% of 1985



Selected U.S. Agricultural Markets

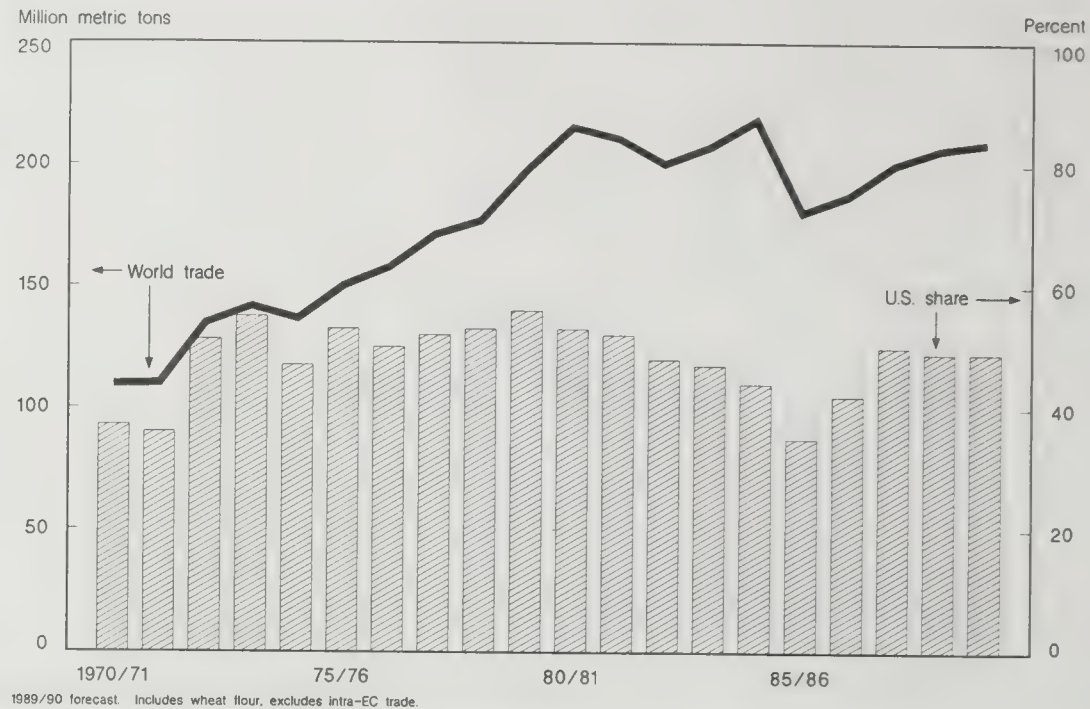
% of 1985



T24

Total world grain trade is up: U.S. share at 50 percent

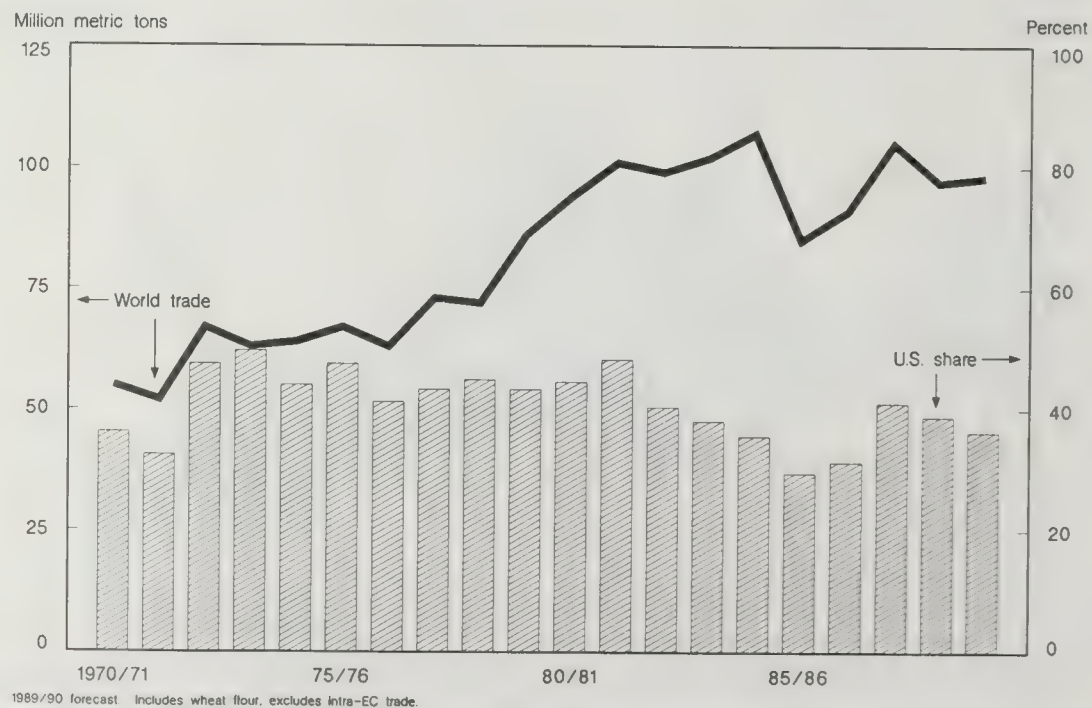
World 1989/90 grain trade is forecast up 2 percent from last year. The United States will capture almost 50 percent of world trade in 1989/90, compared with only 35 percent in 1985/86.



T25

Slight increase in world wheat trade: U.S. share declines

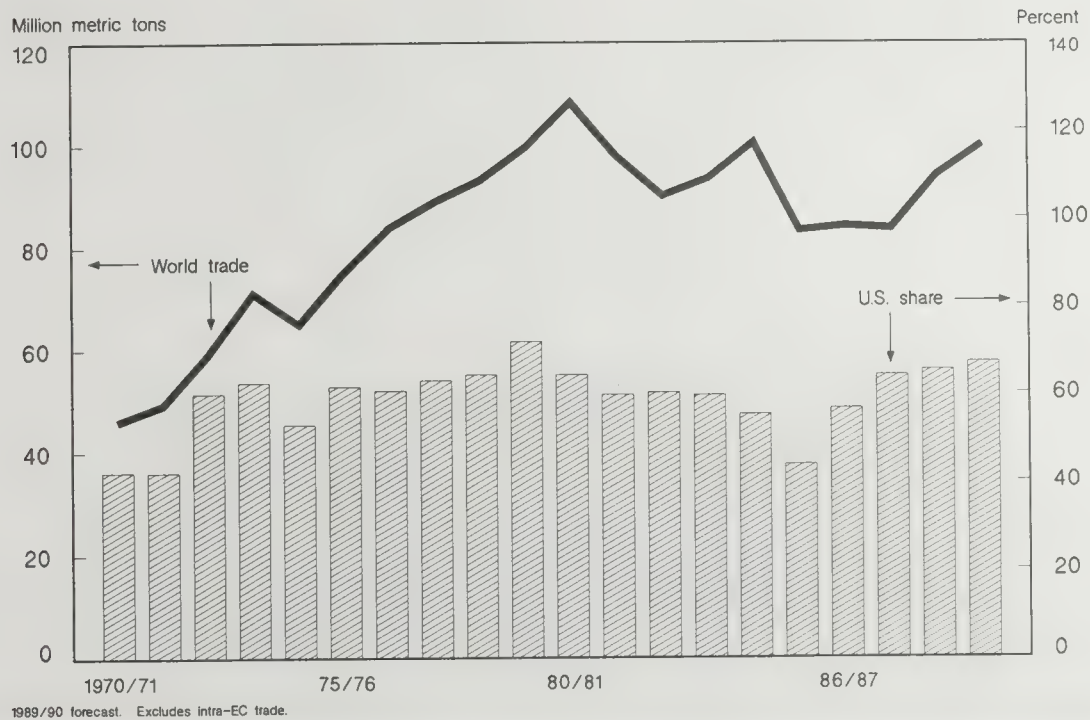
World wheat production is up 7 percent and foreign output is 6 percent above last year due to larger crops in Canada, India, the USSR, China, the EC, and elsewhere. The U.S. share of world wheat trade may drop 3 percent in 1989/90.



T26

World feed grain trade increases: U.S. share near 67 percent

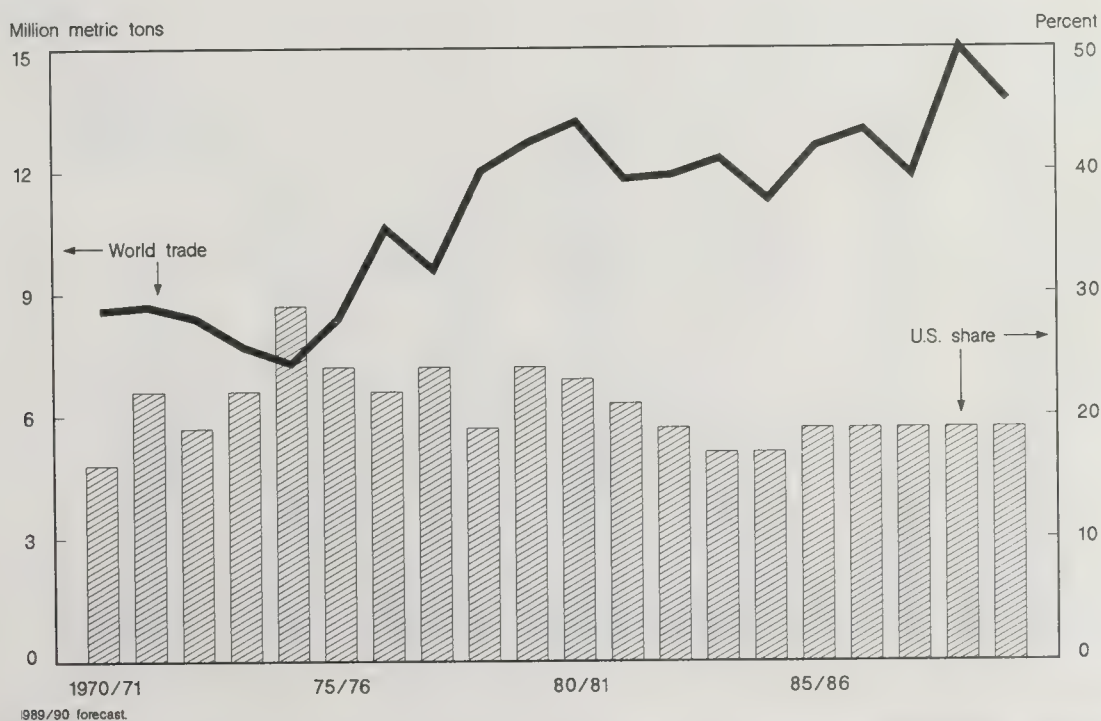
World feed grain production and trade rose in 1989/90. U.S. production rose 48 percent and U.S. trade share is up near 70 percent.



T27

World rice trade drops: U.S. share holds steady

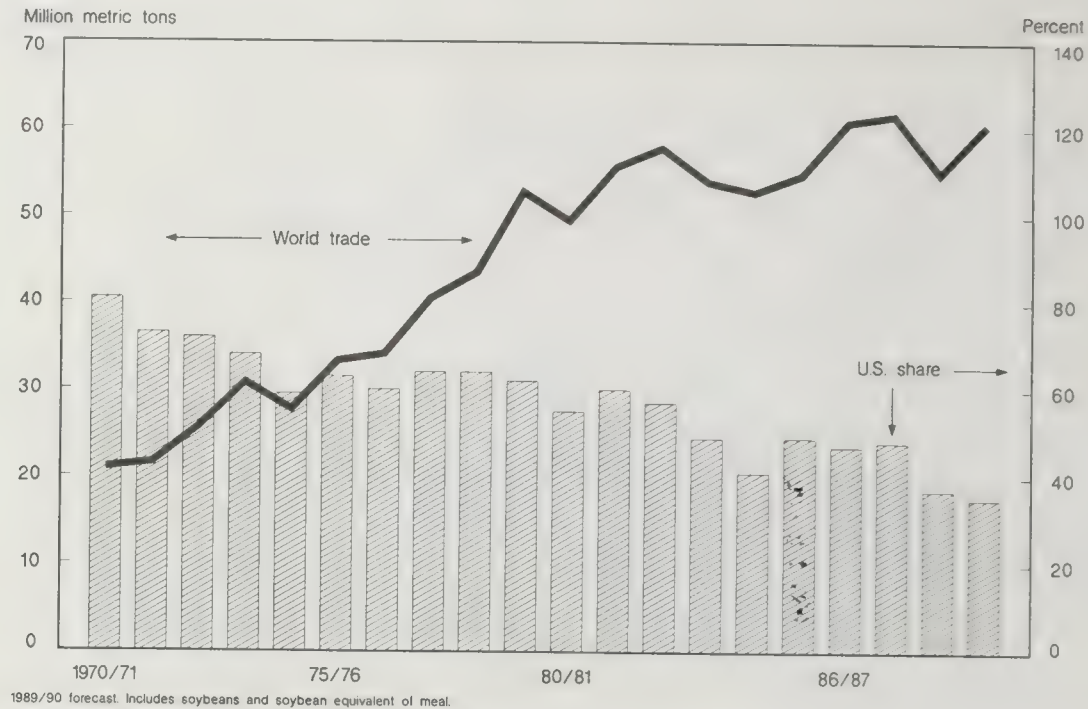
World rice trade is projected to drop 9 percent from 1988/89, but the U.S. share may hold at 19 percent. Global 1989/90 rice production is up 3 percent because of record foreign production.



T28

World soybean trade rebounds: U.S. share continues decline

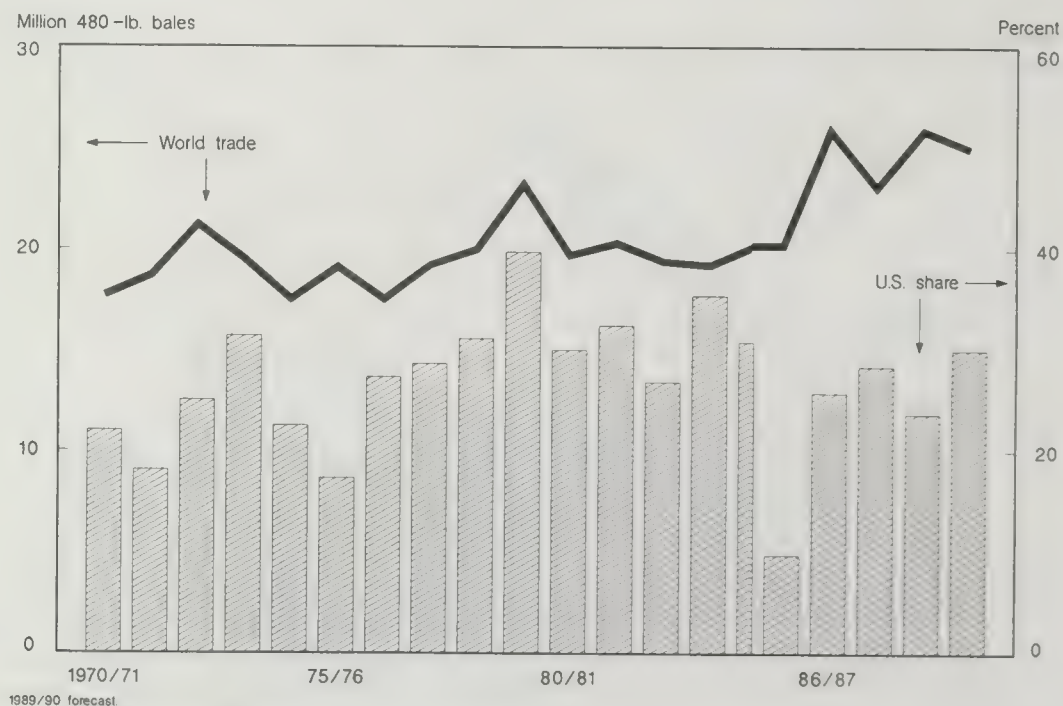
World soybean trade is forecast just below 1987/88's record level of 62 million tons. Larger U.S. and world supplies have helped this year's trade recovery.



T29

World cotton trade is high: U.S. share improves

World cotton trade is high because of strong demand, but stocks are the tightest they have been in several years. U.S. export share climbed to 31 percent, nearly 7 percentage points from last year.



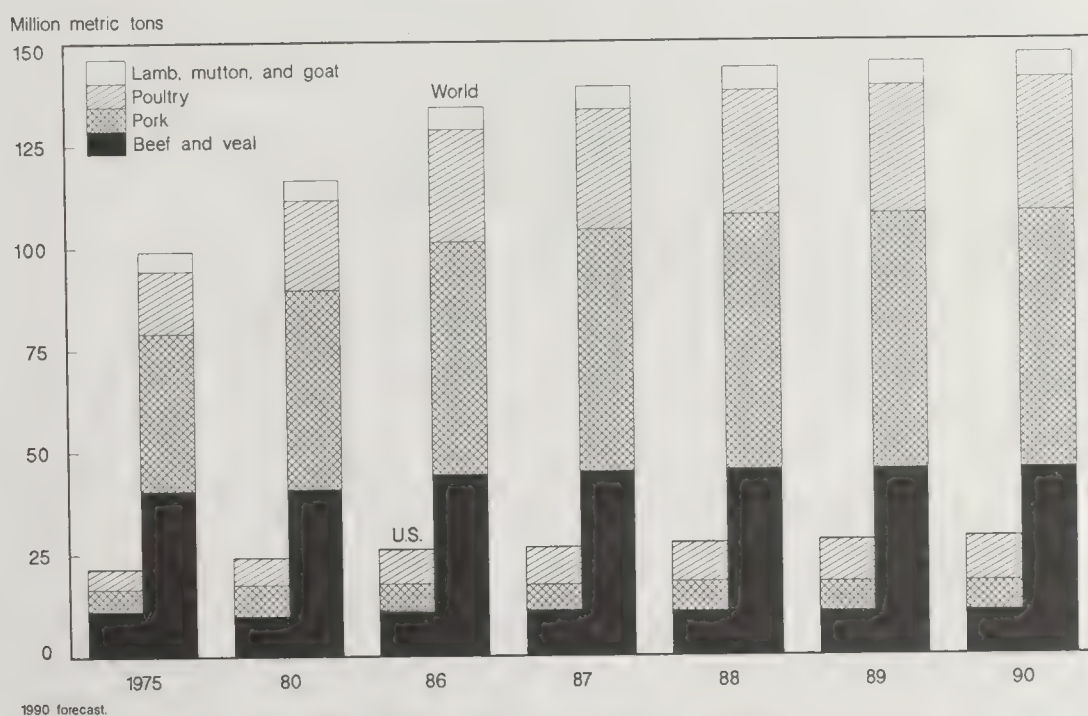
Meat, Livestock, and Dairy Production

U.S. total meat production may rise over 2 percent above the 1989 record with total exports reaching 2.6 billion pounds, more than double the 1986 level. Reflecting larger poultry supplies, per capita meat consumption could surpass the past record levels by 2-3 pounds. Hog prices may rise while cattle prices increase slightly and poultry prices decline.

T30

U.S. and world meat production reach new highs

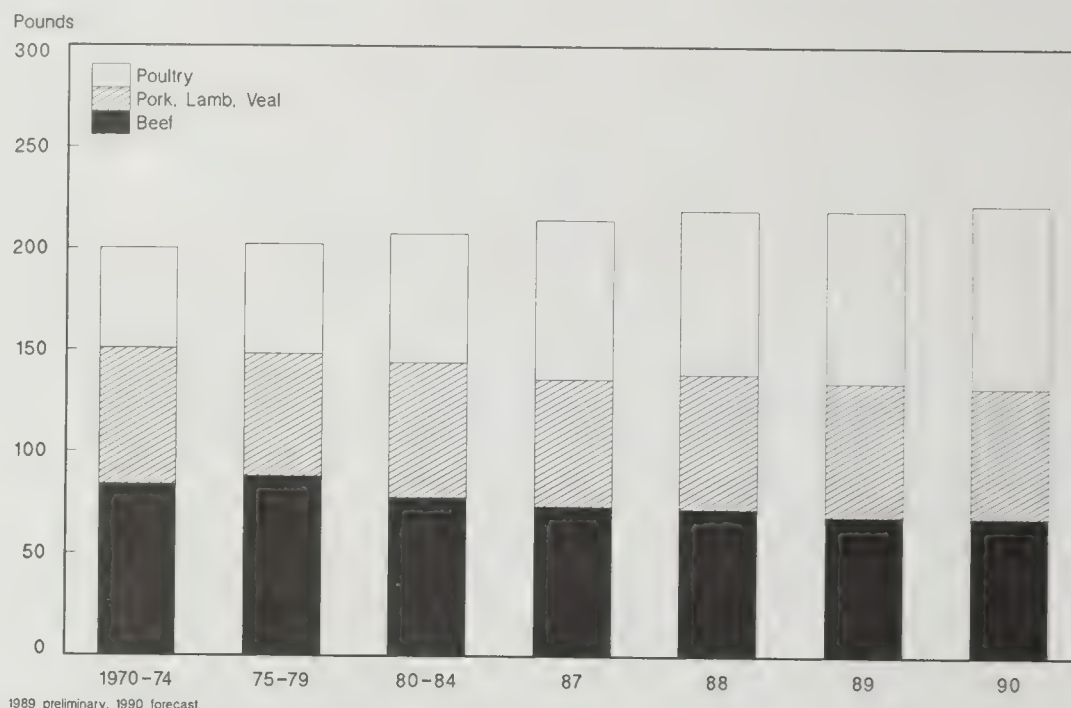
World meat production is rising in 1990, with most of the gain coming from poultry. Pork production may be up a little while beef remains near the 1989 level.



T31

U.S. per capita meat consumption rising due to high poultry consumption

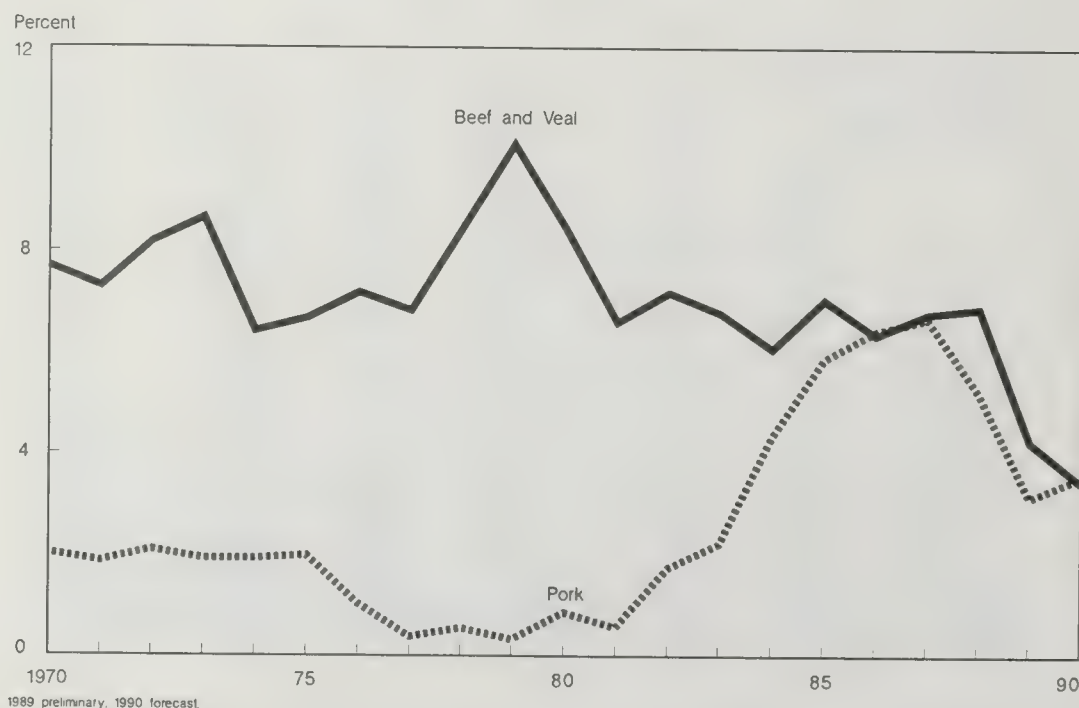
Per capita consumption is expected to increase in 1990 to a new record, surpassing the 1988 total of 219.7 pounds by 2-3 pounds. Increases in poultry more than offset beef and pork declines.



T32

Net meat imports decline as percent of U.S. production

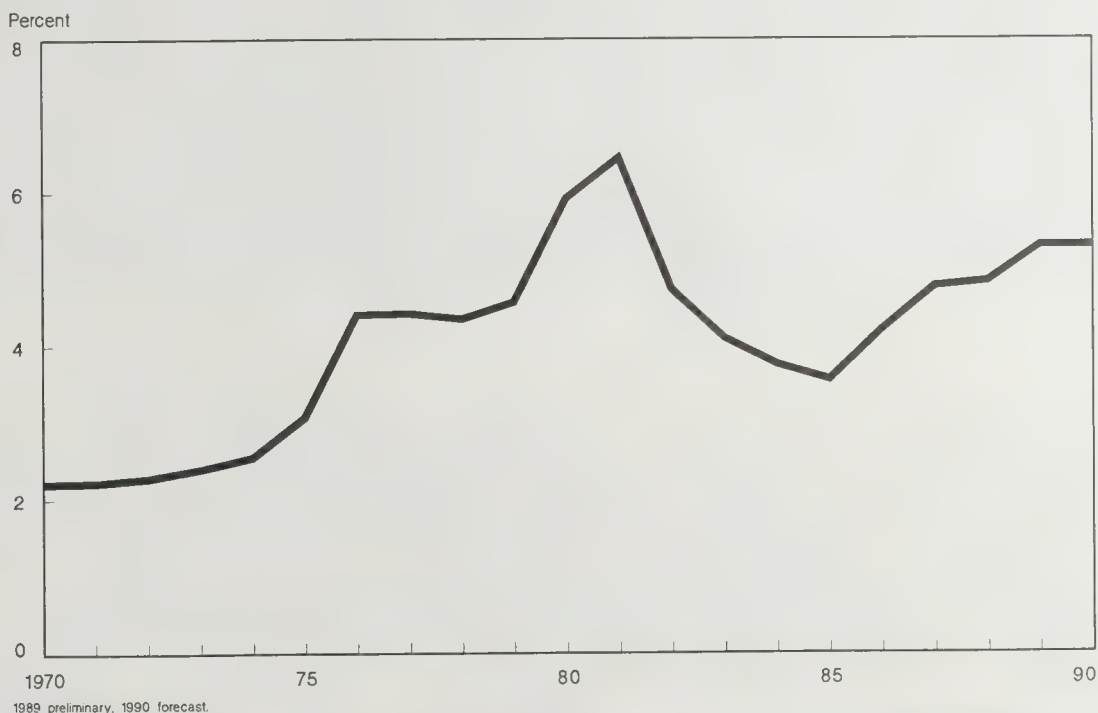
Beef imports declined to 2.2 billion pounds in 1989, or nearly 9 percent of consumption. Pork imports declined about 20 percent in 1989, equaling over 5 percent of pork consumption.



T33

Net poultry exports expanding as percent of U.S. production

Actual poultry meat exports rose 20 percent in 1989 and actual broiler exports, which account for most of the poultry meat exports, rose more than 25 percent.



T34

U.S. meat production, imports, and exports have favorable outlook

U.S. beef exports increased more than 50 percent in 1989 and were a record. Pork exports were up more than a third in 1989, but a decline is likely this year. Total production and exports are steadily rising.

Item	1980	1986	1987	1988	1989 ^P	1990 ^F
Million pounds						
Beef:						
Production	21,643	24,371	23,566	23,589	23,138	23,540
Imports	2,064	2,129	2,269	2,379	2,155	2,115
Exports	173	521	604	680	1,067	1,200
Pork:						
Production	16,616	14,063	14,374	15,684	15,820	15,586
Imports	550	1,122	1,195	1,137	900	940
Exports	252	286	109	195	265	255
Poultry:						
Production	14,541	18,215	20,065	20,786	22,247	23,632
Imports	0	0	0	0	0	0
Exports	695	609	800	842	1,035	1,108
Total meats:						
Production	53,519	57,511	58,749	60,790	61,905	63,468
Imports	2,668	3,319	3,532	3,594	3,117	3,118
Exports	1,126	1,222	1,521	1,728	2,369	2,564
Net imports	1,542	2,097	2,011	1,866	748	554
Percent						
Net imports as percent of production	2.9	3.6	3.4	3.1	1.2	.9

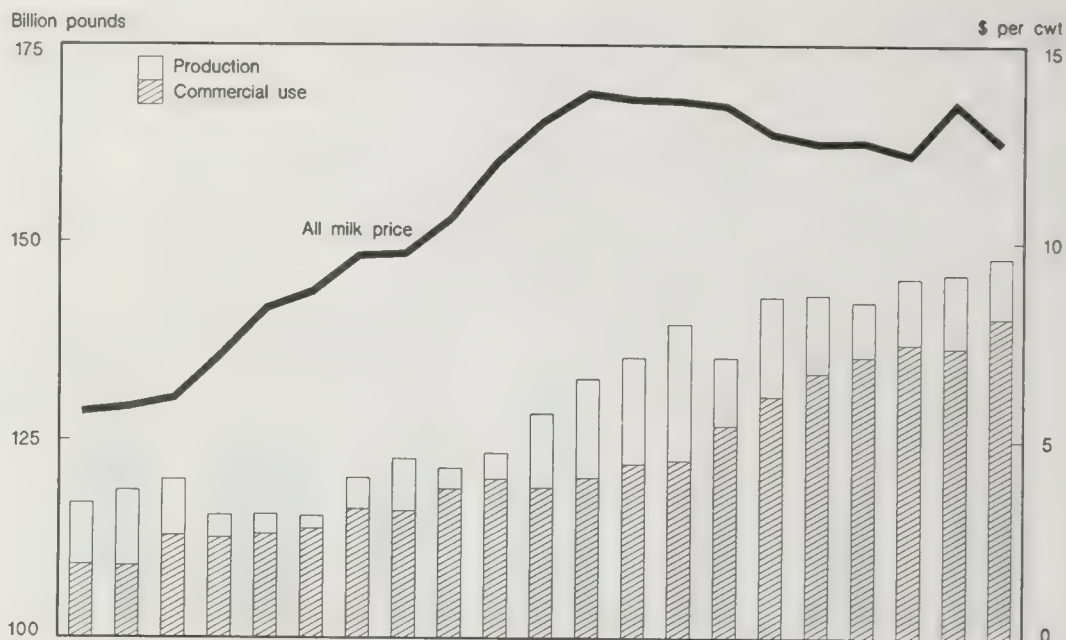
P=Preliminary. F=Forecast.

The United States produces all the poultry meat for its domestic consumption.

T35

U.S. milk production and use should increase while prices decrease

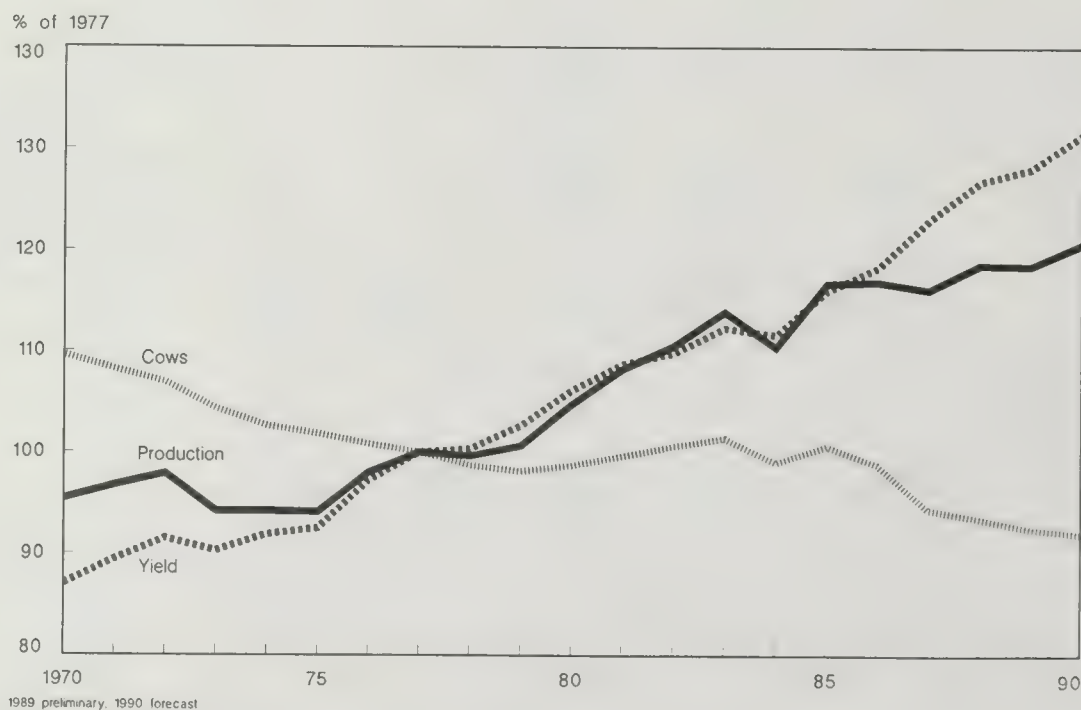
Milk prices in 1989 averaged about \$1.25 per hundredweight above the 1988 level. Commercial use of dairy products was down slightly in 1989. Milk prices are expected to decline in 1990.



T36

Milk production and milk per cow on the rise

Milk production in 1990 is expected to increase 1-3 percent as declines in cow numbers moderate and milk output per cow increases.



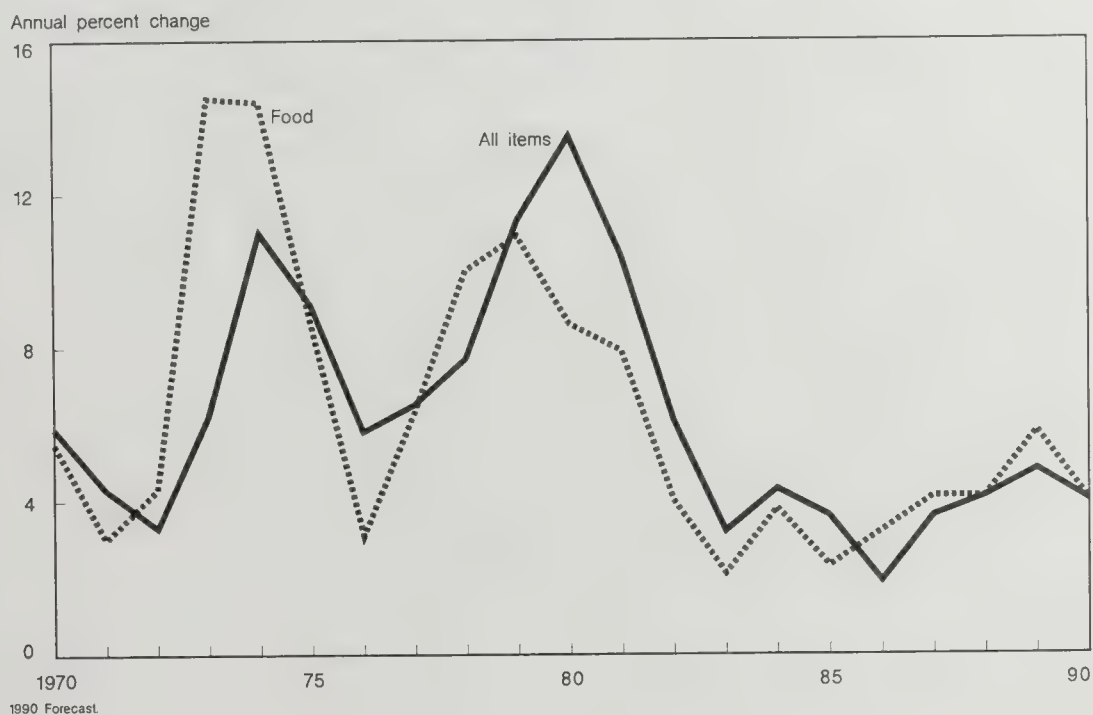
Food Prices

Upward pressure on food prices may ease in 1990. The Consumer Price Index for food could rise by 3-5 percent in 1990, compared with an increase of 5.8 percent in 1989. Supplies of most foods will be ample, led by large supplies of poultry. Growth in consumer demand may slow from the past 2 years, and a lower rate of inflation will slow increases in food industry costs.

T37

Consumer Price Index

The Consumer Price Index for food is expected to rise 3-5 percent in 1990, a slower pace than the 5.8-percent rise in 1989. Food processing and distributing costs will be moderated by a lower rate of inflation in the general economy in 1990, holding down the nonfarm component of food costs.



Percent changes in the Consumer Price Index

Item	1980	1986	1987	1988	1989	1990 ^F
Percent						
All items	13.5	1.9	3.6	4.1	4.8	4.0
Housing	15.7	2.9	3.0	3.8	3.8	NA
Medical care	10.9	7.5	6.6	6.5	7.7	NA
Transportation	17.8	-3.9	3.0	3.1	5.0	NA
Energy	34.7	-13.2	.5	.8	5.6	NA
Food ¹	8.6	3.2	4.1	4.1	5.8	3-5

NA=Not available. ¹ Excludes alcoholic beverages. F=Forecast.

Background Charts for U.S. Agriculture

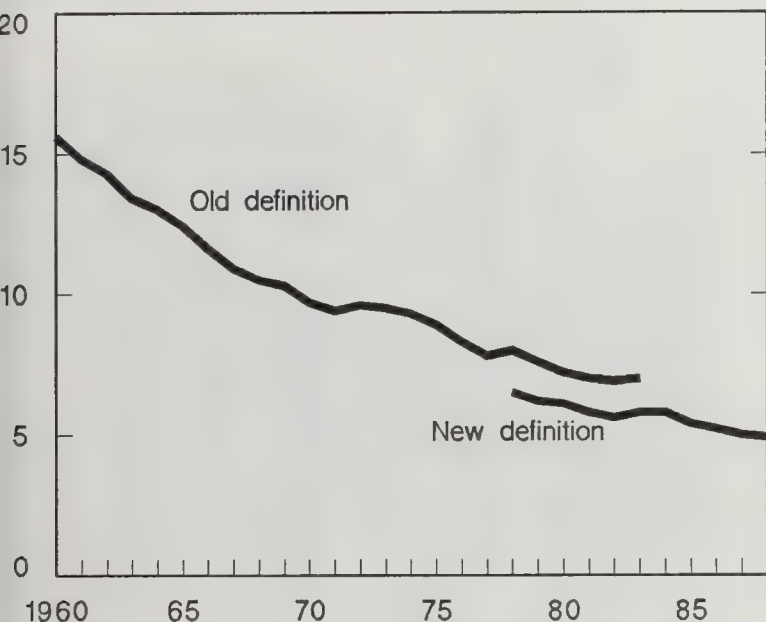


Farm Population

About 4.8 million people, or 2 percent of the Nation's total population, lived on farms in 1988. The farm population is about 5 years older (median age) than the rest of the U.S. population. The total number of farms and the farm population seem to have stabilized in the late 1980's.

Chart 1
Farm population

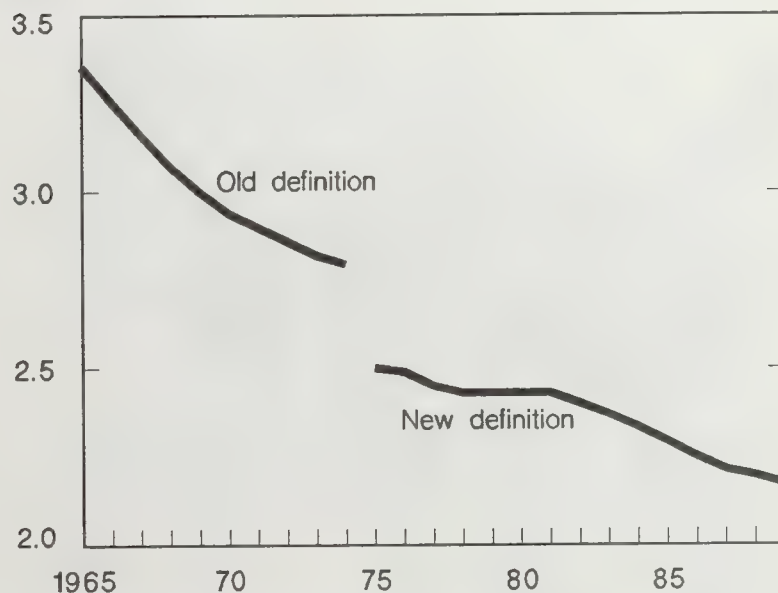
Million persons



The farm population includes all people living on rural farms. For farm definitions, see 1982 Census of Agriculture. Source: Bureau of the Census.

Chart 2
Number of farms

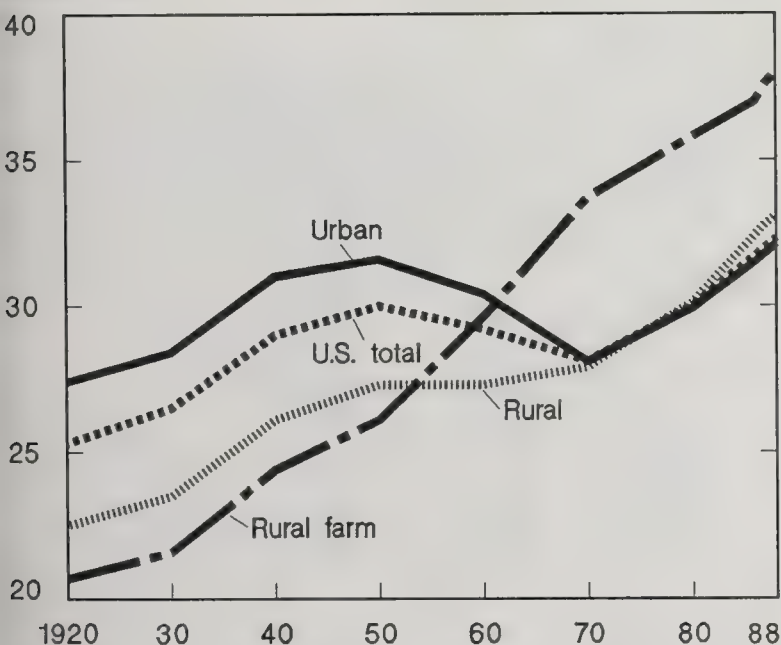
Million



Starting with 1975, a farm is a place that sells \$1,000 or more of agricultural products during the year. For more information on farm definitions, see 1982 Census of Agriculture. Source: Bureau of the Census.

Chart 3
Median age of the population by residence

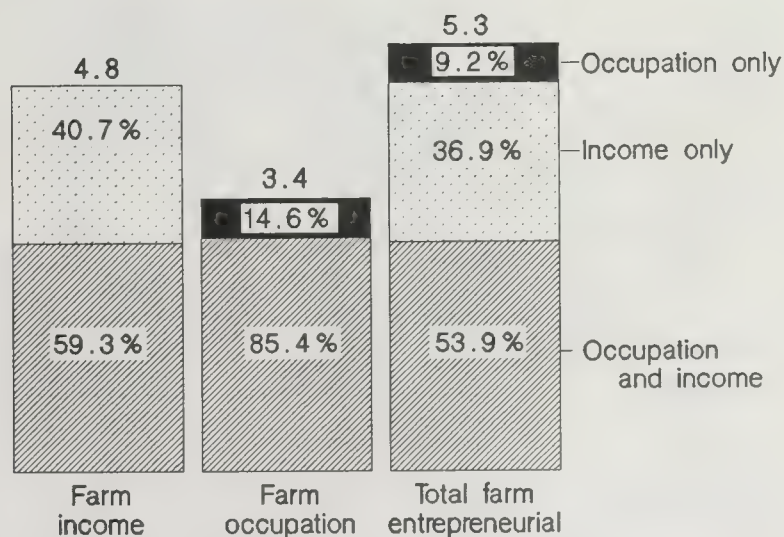
Median age



Source: Bureau of the Census.

Chart 4
Composition of the farm entrepreneurial population

Million persons

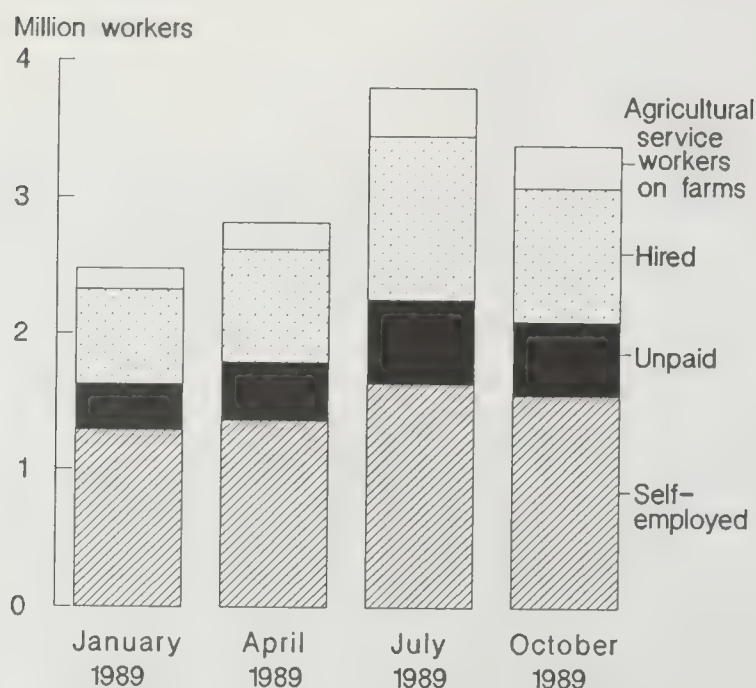


March 1988 data. Total farm entrepreneurial population consists of all persons in households where at least one member is employed primarily as a farm operator or manager and/or receives farm self-employment income. Source: Bureau of the Census.

Farm Labor

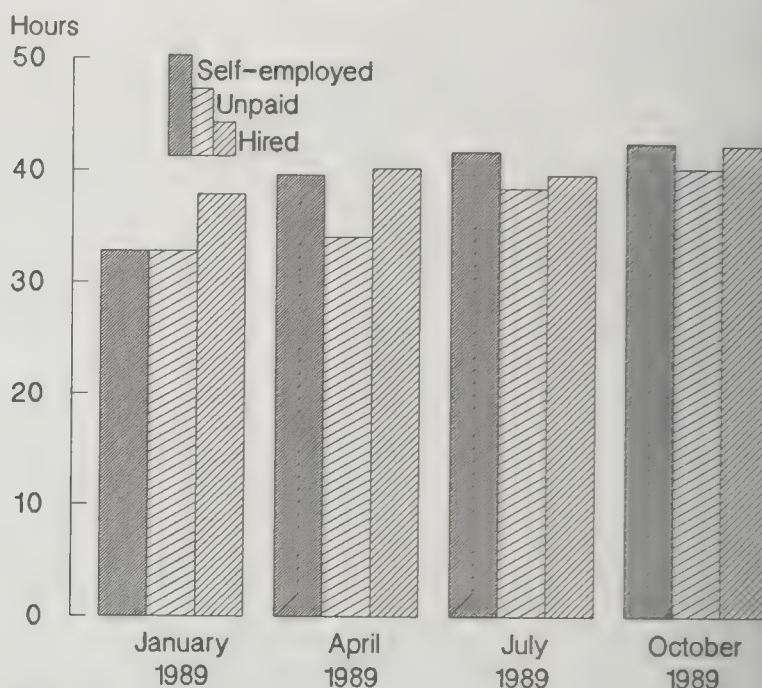
Farm employment is highly seasonal, with heaviest use of farm labor and most hours worked coming in July and October. Supervisory worker wage rates were higher than those of other farmworkers. Most hired farmworkers work on farms with gross sales value of \$250,000 and over. Farm operators and family members make up more than half of all U.S. farmworkers.

Chart 5
U.S. farm employment



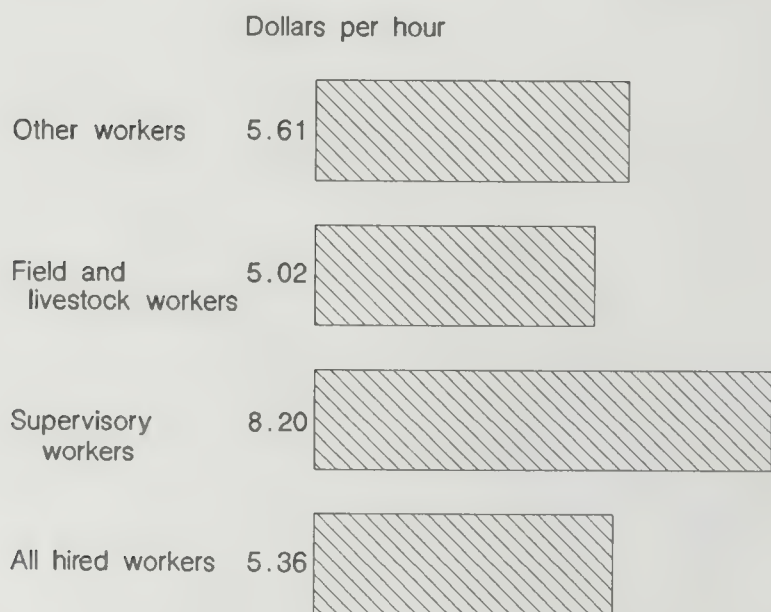
Source: Farm Labor, NASS.

Chart 6
Hours worked per week on U.S. farms



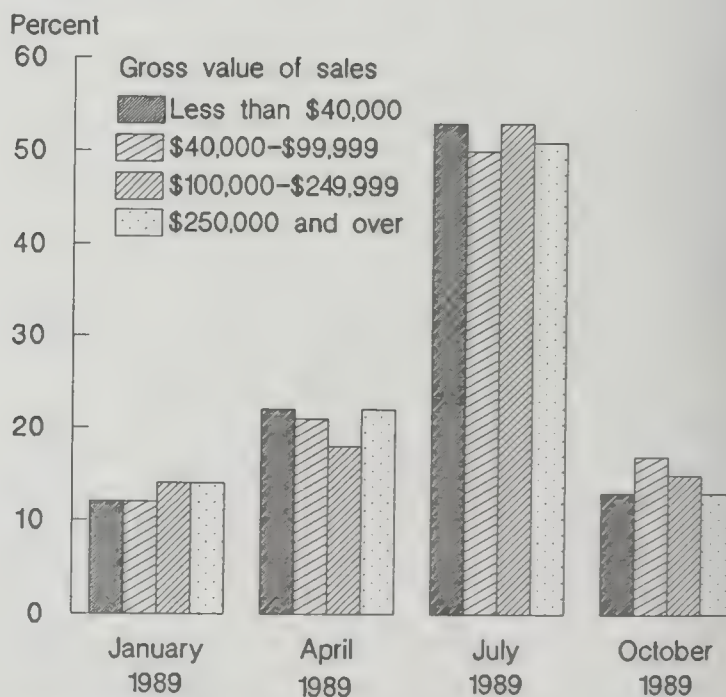
Source: Farm Labor, NASS.

Chart 7
U.S. annual average farm wage rates, 1989



Source: Farm Labor, NASS

Chart 8
Distribution of hired workers by farm size

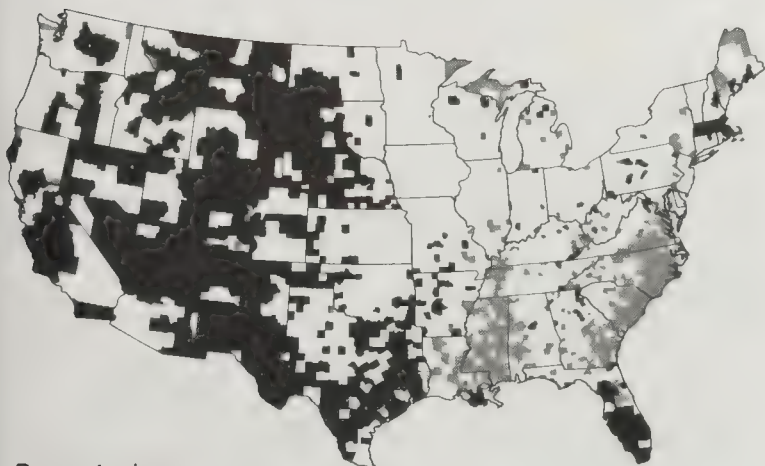


Source: Farm Labor, NASS

Regional Farm Structure

Farm numbers in the West rose from 1982 to 1987, but increases in average acre size of farms were most pronounced in the Midwest and the Northeast. The highest proportion of commercial farms is in farming-dependent counties. There are 514 farming-dependent counties where farming contributed at least 20 percent of the county's labor and proprietor income in 1980-84, and 540 farming-important counties where farming contributed 10-19 percent of the county's labor and proprietor income.

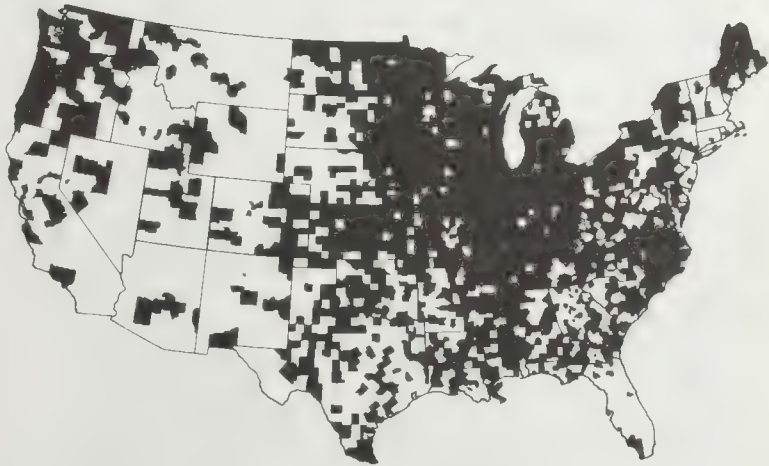
Chart 9
Change in farm numbers, 1982-87



Percent change

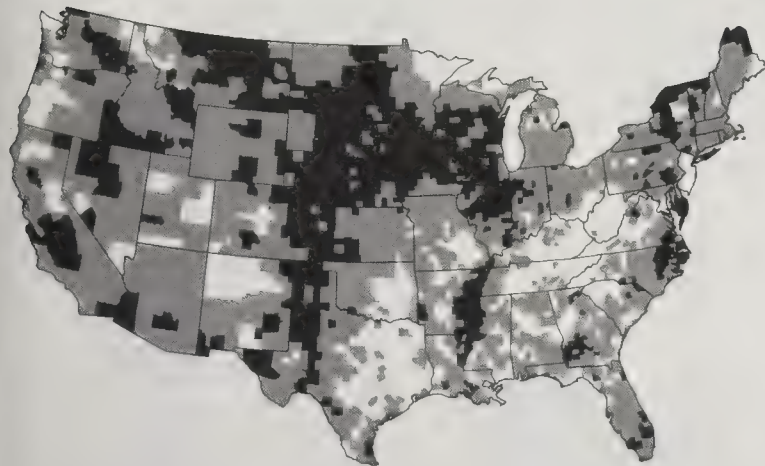
- Increases to 45
- Declines to -16.7
- 16.7 to -52.8

Chart 10
Change in average farm size, 1982-87



Declines Increases

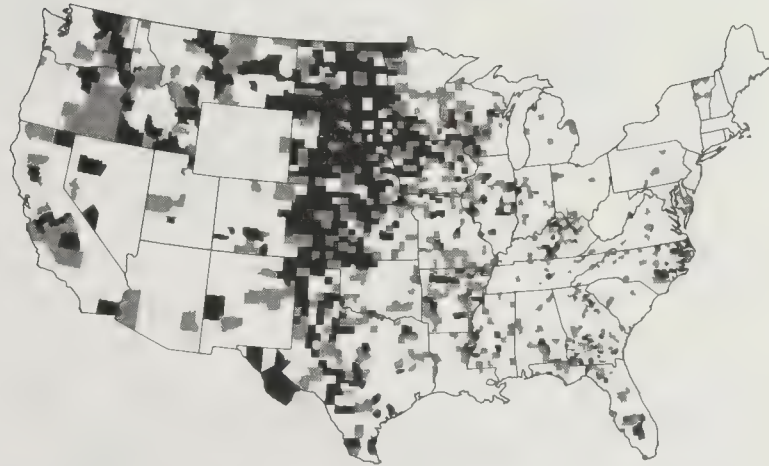
Chart 11
Most and least commercial farm counties, 1987



Percent of farms with more than \$50,000 sales

- More than 35.6
- 10.2-35.6
- Less than 10.2

Chart 12
Local dependence on farming, 1980-84



Farming-dependent counties
Farming-important counties
Not-farming-dependent counties

Income

Gross farm income went up 3.5 percent from 1987, totaling \$177.6 billion. Net farm income and returns to operators dropped 3.1 and 4.3 percent from 1987. Net cash income, cash-flow, and business income increased 4.1, 3.8, and 4.8 percent respectively. Gross farm income and production expenses rose 3.5 and 6 percent in 1988.

Chart 13
Components of gross farm income

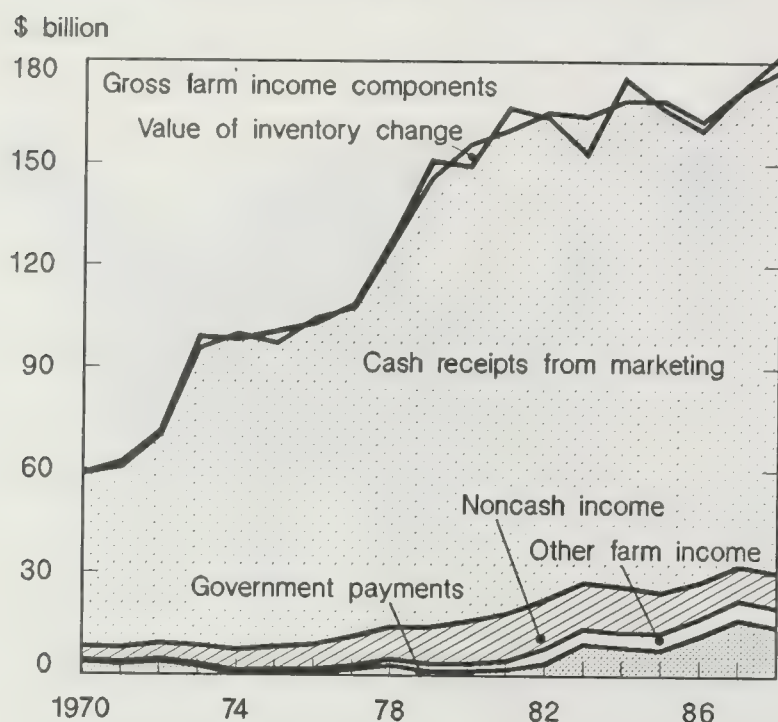
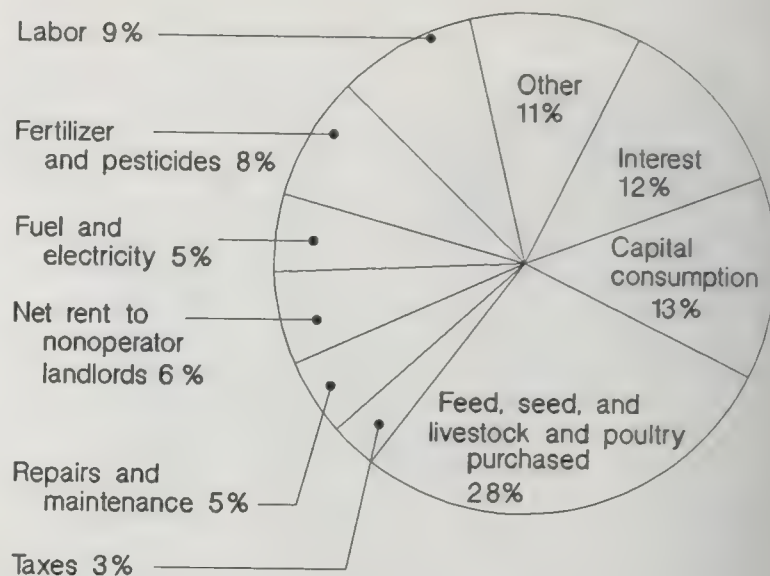


Chart 14
Components of farm production expenses



1988 data. Includes operator farm dwellings. Other expenses include machine hire and customwork; marketing, storage, and transportation; and miscellaneous.

Chart 15
Measures of farm income

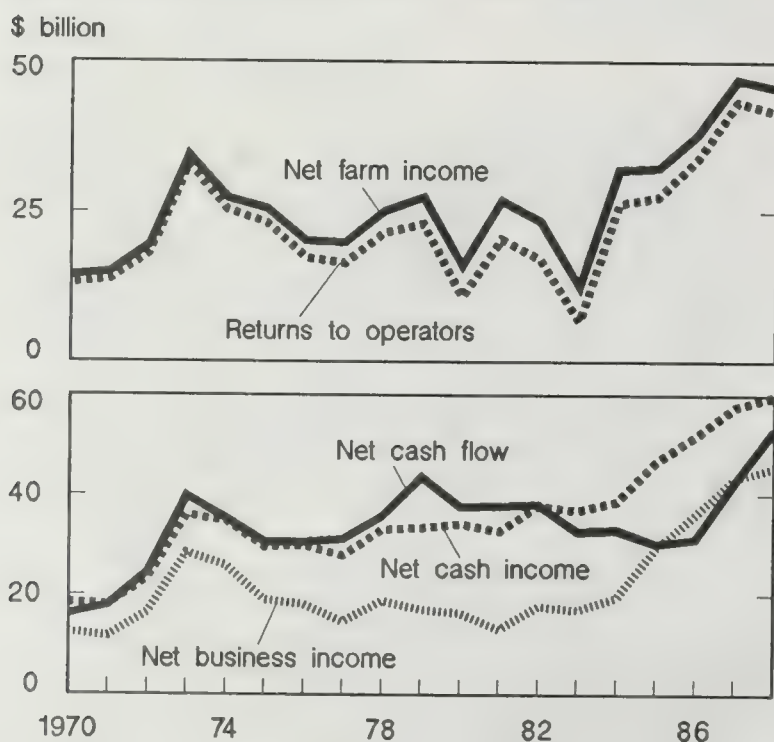
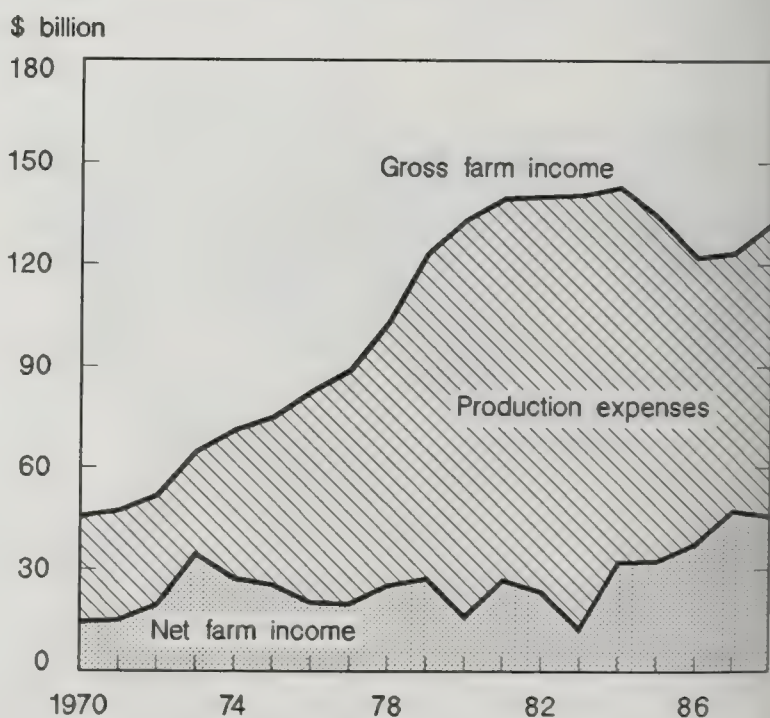


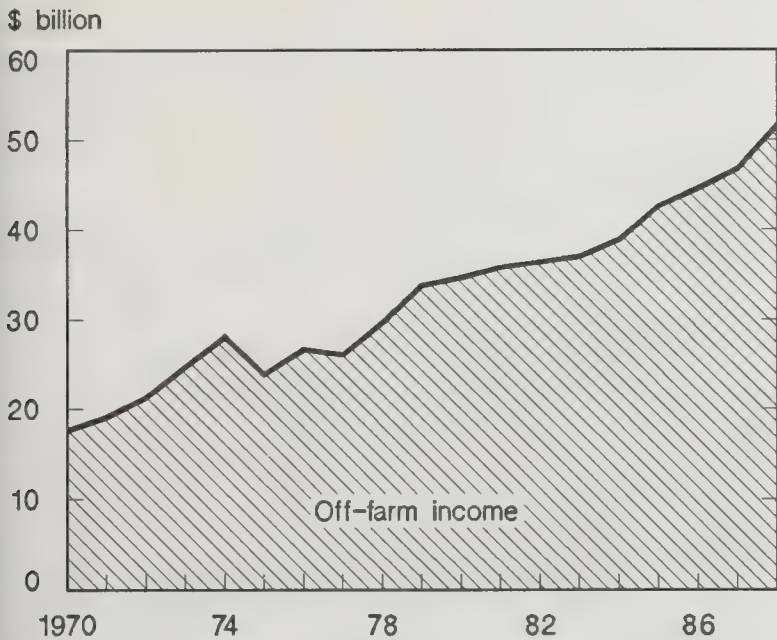
Chart 16
Net farm income



Income

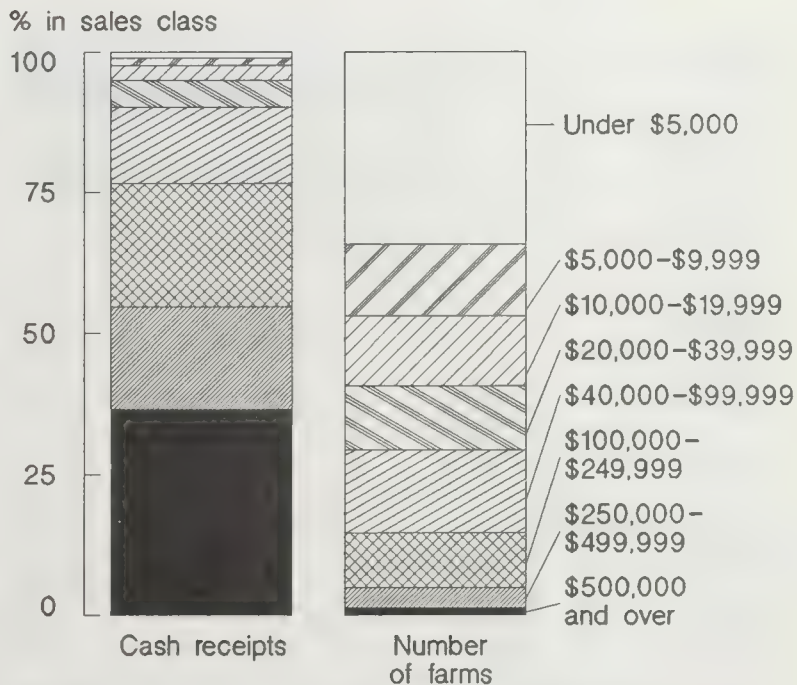
Off-farm income of farm households rose 10.5 percent in 1988. Farms with sales over \$250,000 constituted only 5 percent of all farms, but 55 percent of cash receipts from farm marketings. Over two-thirds of farms were in a favorable financial position in 1988.

Chart 17
Off-farm Income of farm operator households



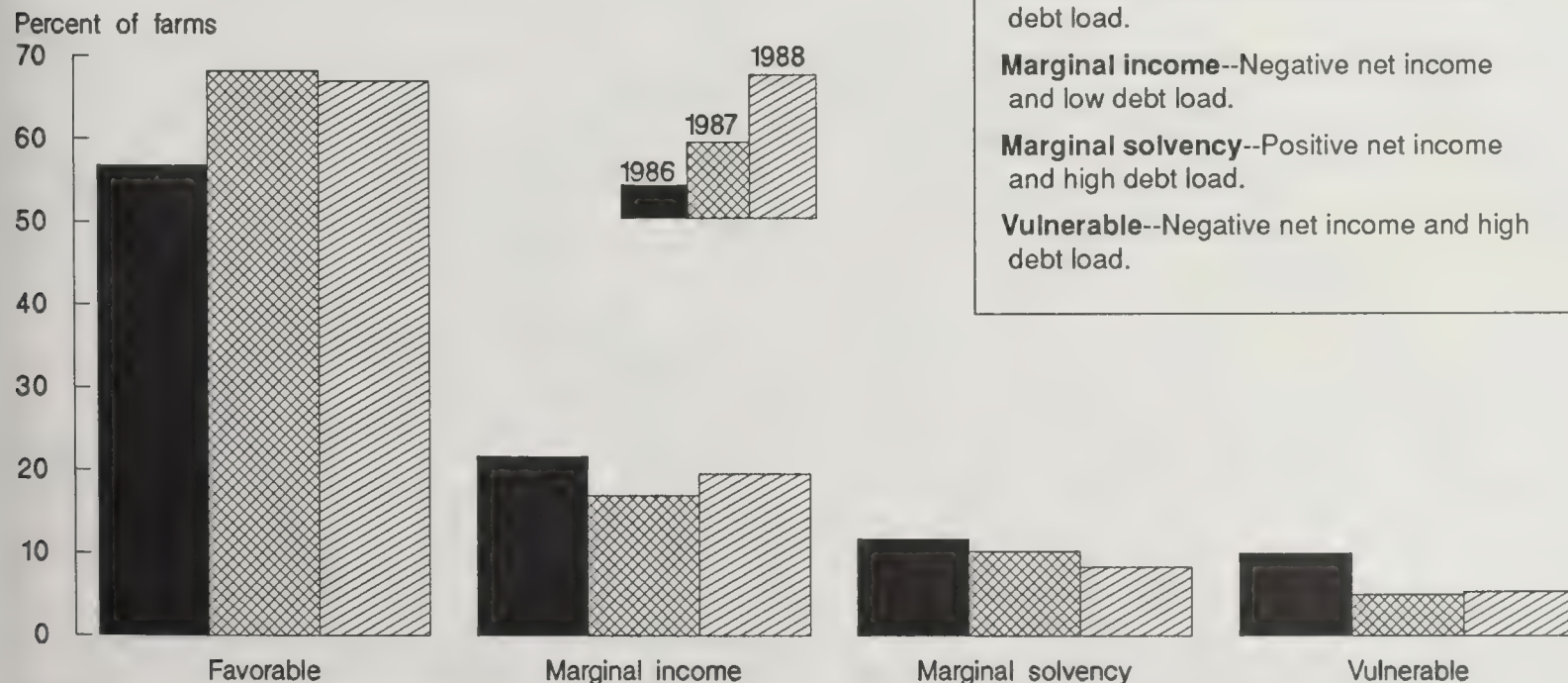
Net cash income includes an adjustment for changes in yearend crop and livestock inventories and represents returns to operator families' labor, capital, and management.

Chart 18
Cash receipts and farms by sales class



1988 data. Cash receipts from farm marketings include net CCC loans.

Chart 19
Distribution of farms by financial position

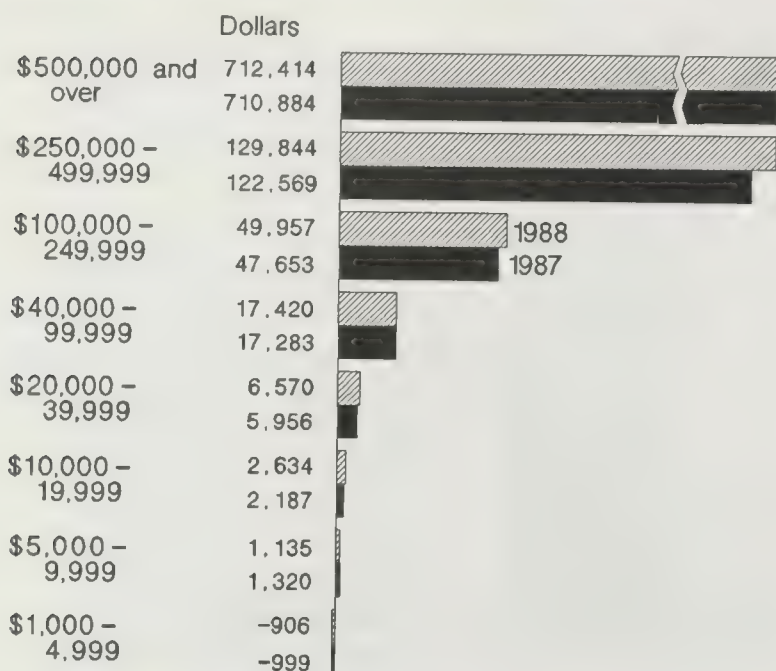


Source: Farm Costs and Returns Surveys, USDA.

Income

The smallest farms averaged negative net farm income while the largest farms averaged about \$712,000 in 1988. Drought in major crop-producing regions contributed to price increases of over 30 percent for wheat, corn, and soybeans. Prices paid by farmers rose 7 percent in 1988, while the prices they received for all farm products rose 9 percent.

Chart 20
Average net farm income by sales class



Net income before adjustment for inventory change.

Chart 21
Prices received by farmers for major commodities

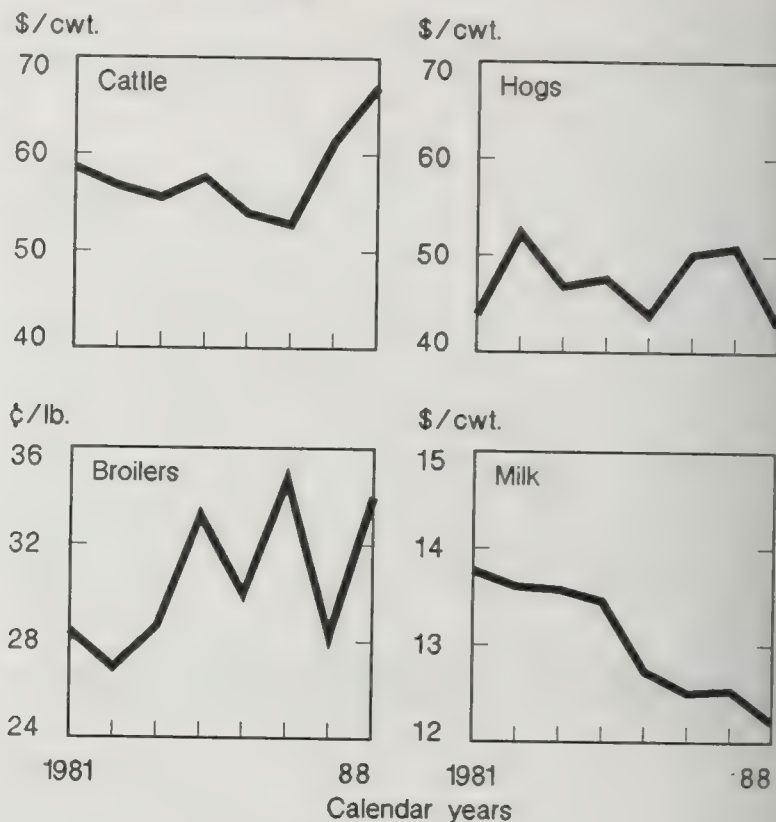
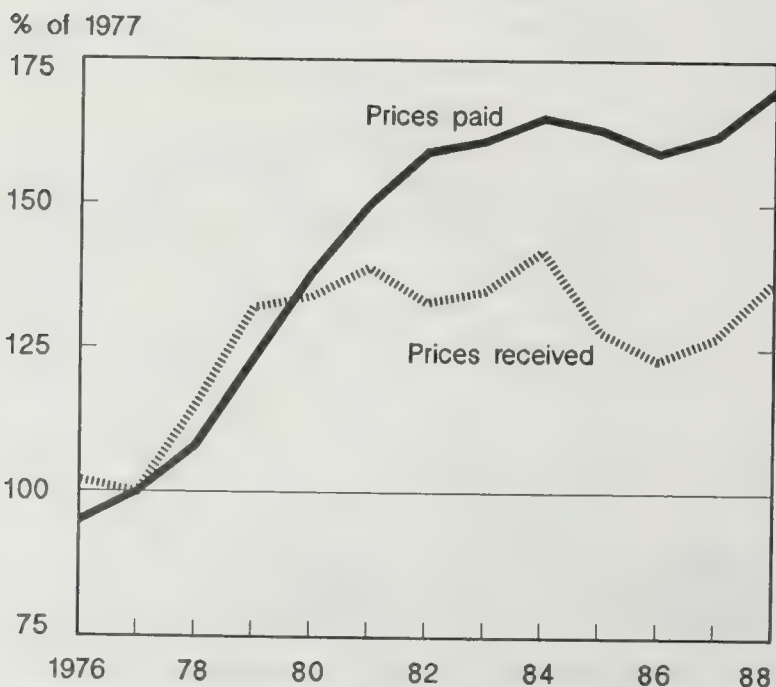
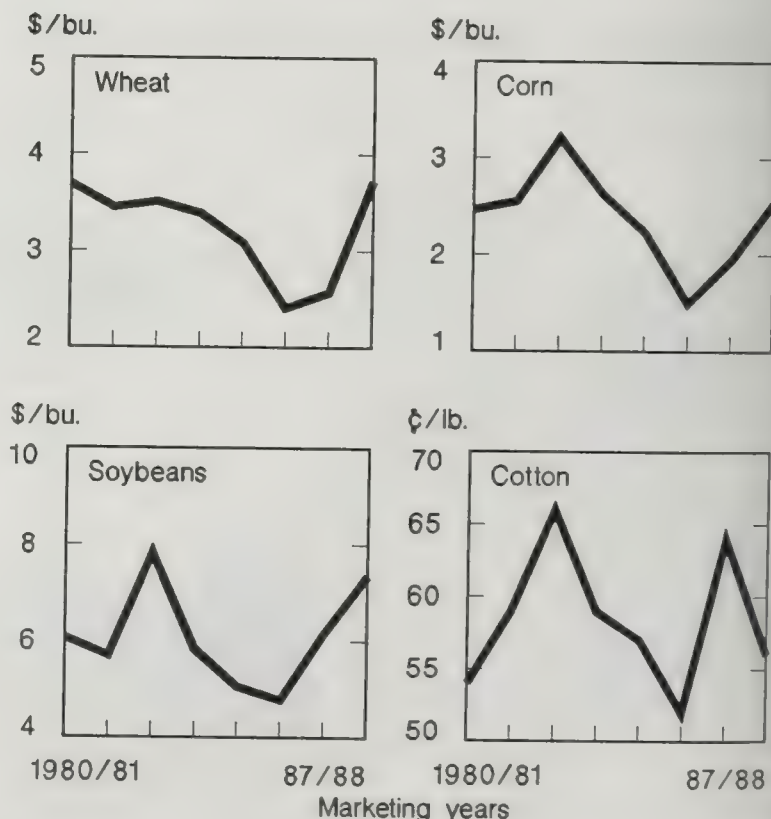


Chart 22
Prices received and paid by farmers



Prices paid includes commodities, services, interest, taxes, and wage rates.



Farm Debt

Both real estate and nonreal estate farm loans fell during 1988, as farmers used increased cash income to pay off loan balances. Farmers' debt-asset ratios fell as farmers paid off more than \$5 billion in farm debt.

Chart 23
Who holds the farm debt

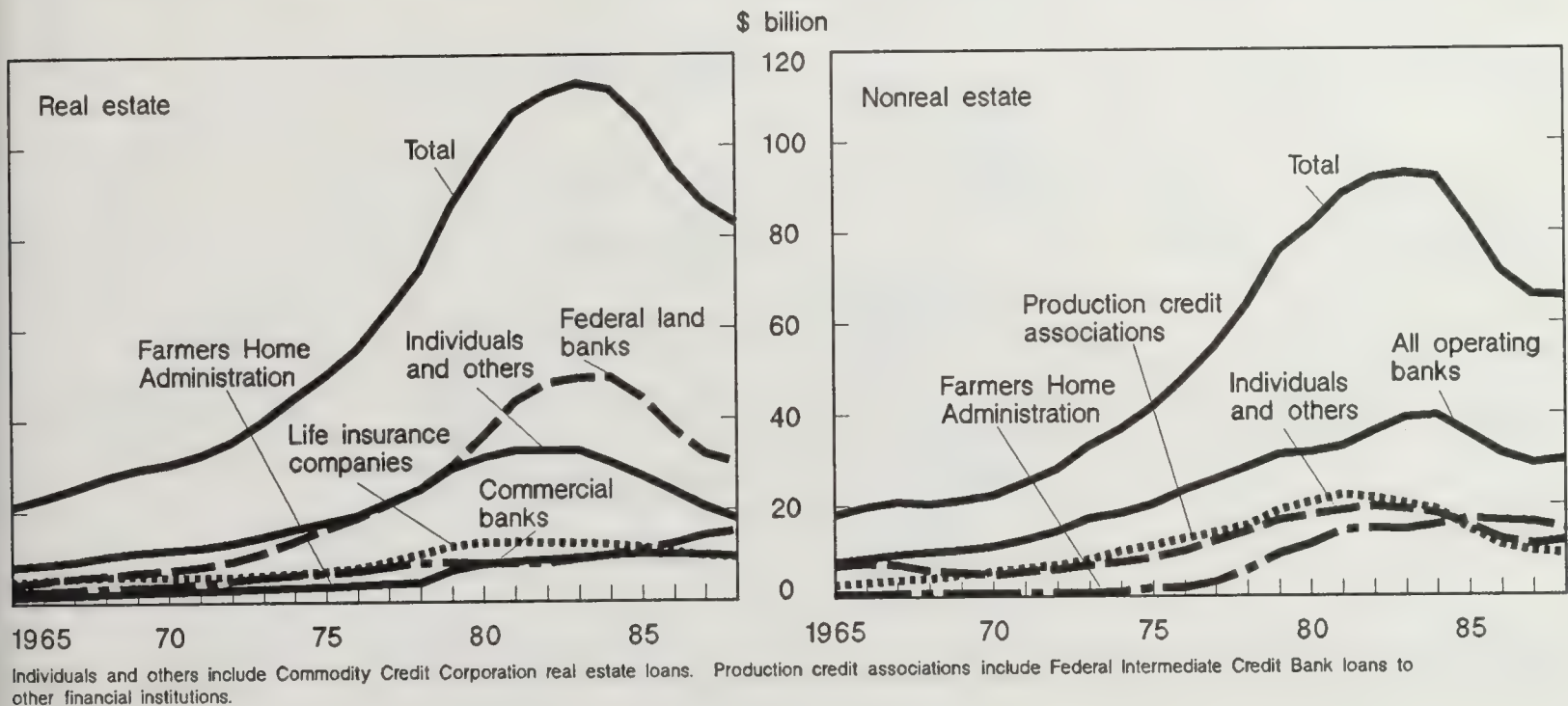


Chart 24
Annual change in farm debt

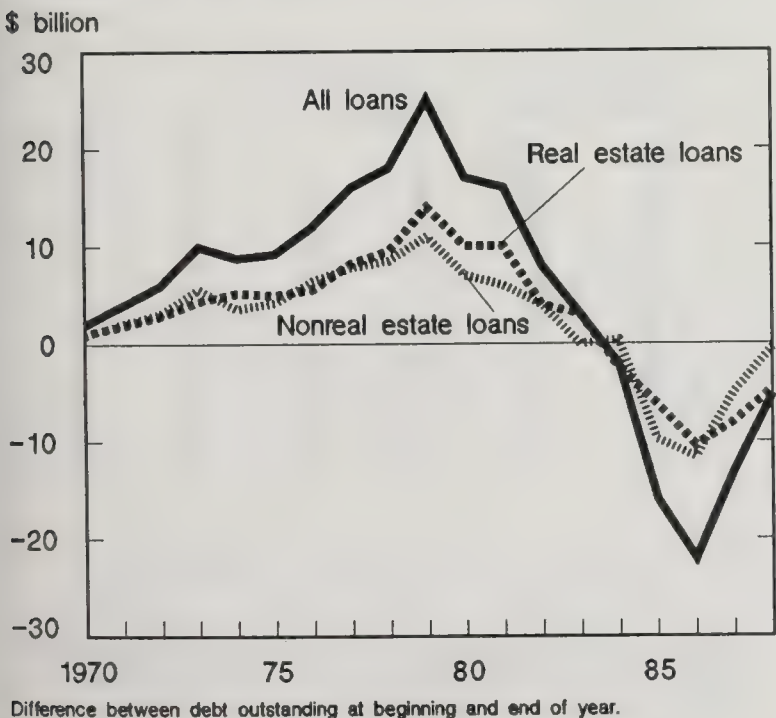
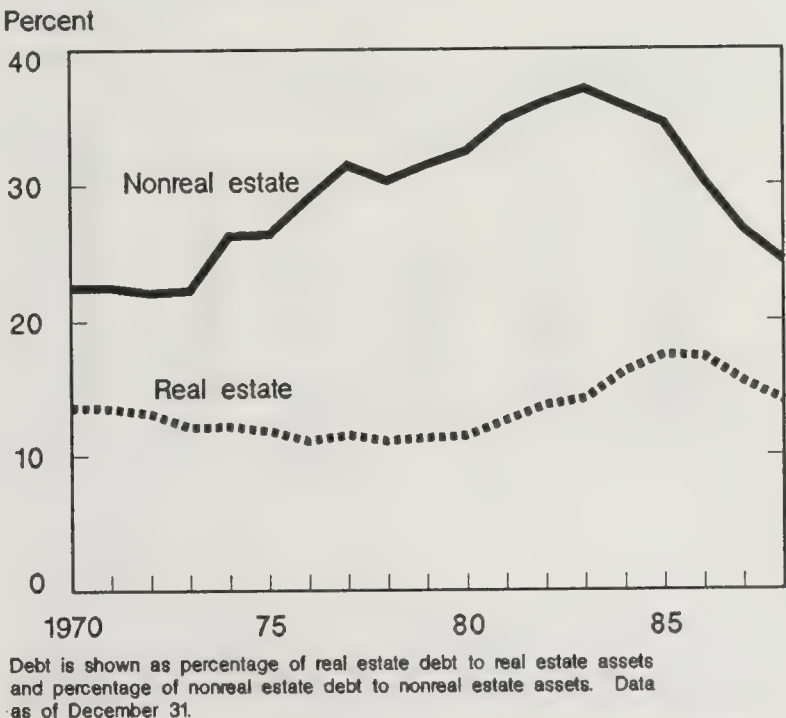


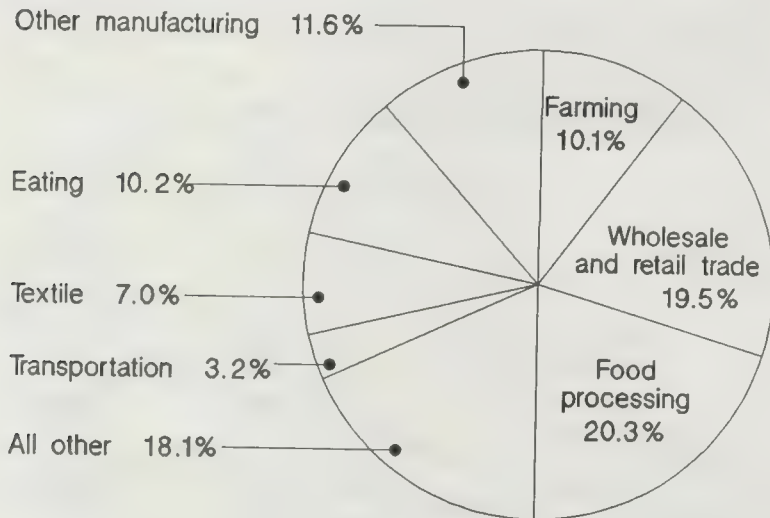
Chart 25
Farm debt as percentage of assets



Food and Fiber System

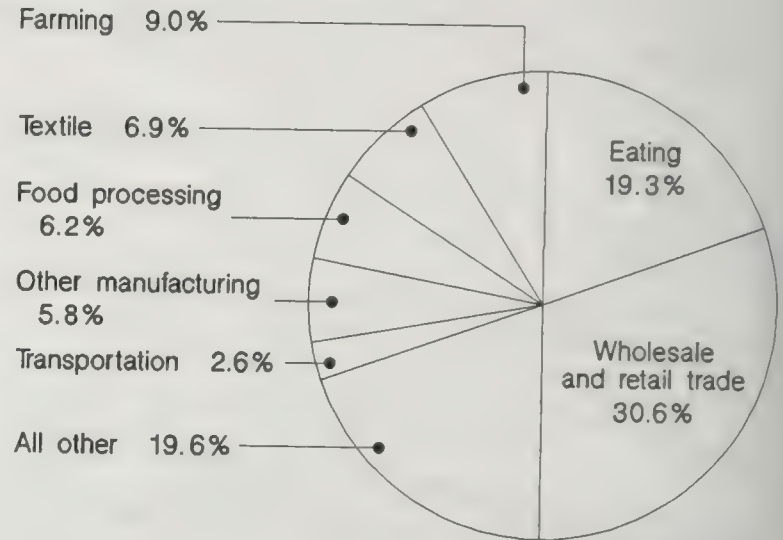
The food and fiber system employed 19.6 million workers in 1988, 16.1 percent of the civilian workforce. But only 9 percent of those workers are in farming, which accounts for just over 10 percent of total output of the U.S. food and fiber sector.

Chart 26
Total output by sectors of the food and fiber system
% of \$ output



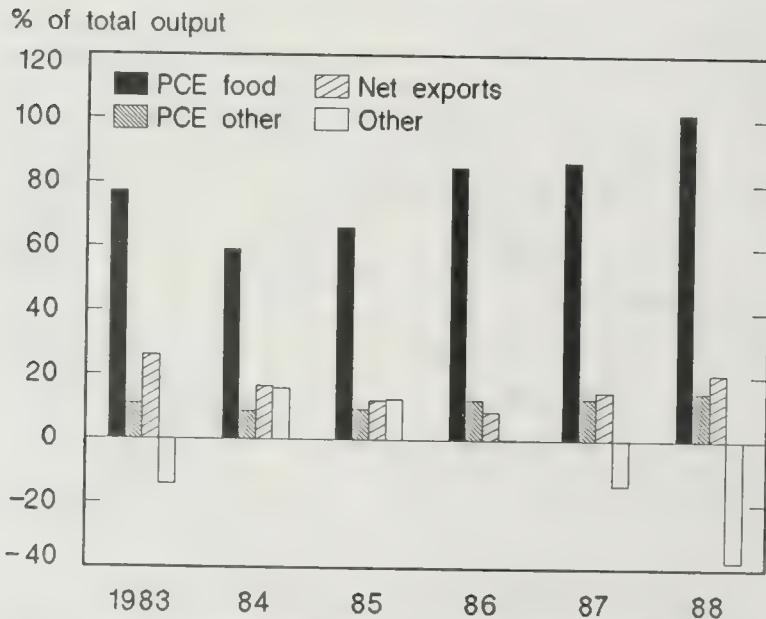
1988 data.

Chart 27
Distribution of food and fiber system employment



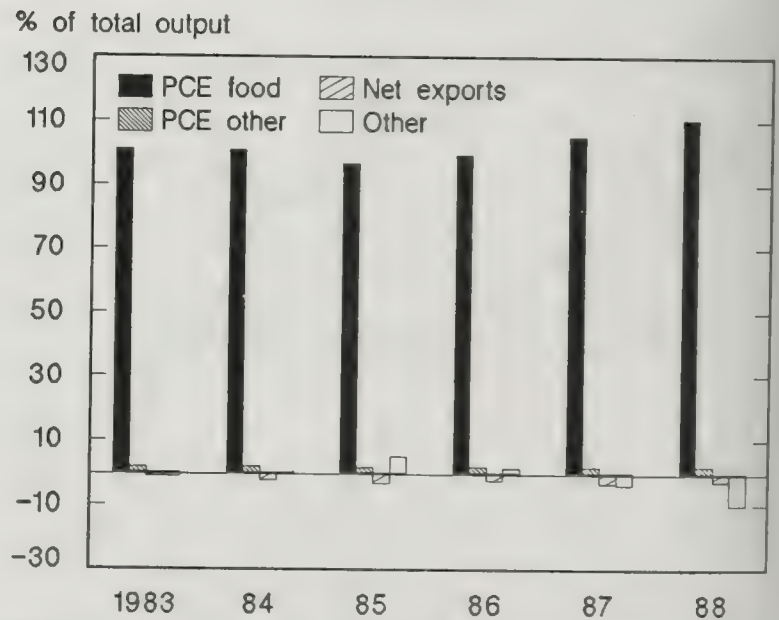
1988 data.

Chart 28
Sources of demand for crop output



PCE is personal consumption expenditures. PCE other includes domestic consumption of tobacco, clothing, shoes, cut flowers, and potted plants. Other includes private and public farm inventory changes, farm capital expenditures, direct government uses, and nonfarm related final demands.

Chart 29
Sources of demand for livestock output



PCE is personal consumption expenditures. PCE other includes domestic consumption of tobacco, clothing, shoes, cut flowers, and potted plants. Other includes private and public farm inventory changes, farm capital expenditures, direct government uses, and nonfarm related final demands.

Agriculture and the General Economy

After the 1970's export boom, the farm sector resumed its historical downward trend as a share of the general economy. In contrast with the 1970's, when rapidly rising prices for farm goods contributed to higher consumer prices, farm prices since 1980 have had a moderating influence on consumer prices.

Chart 30
Gross farm product share of gross national product

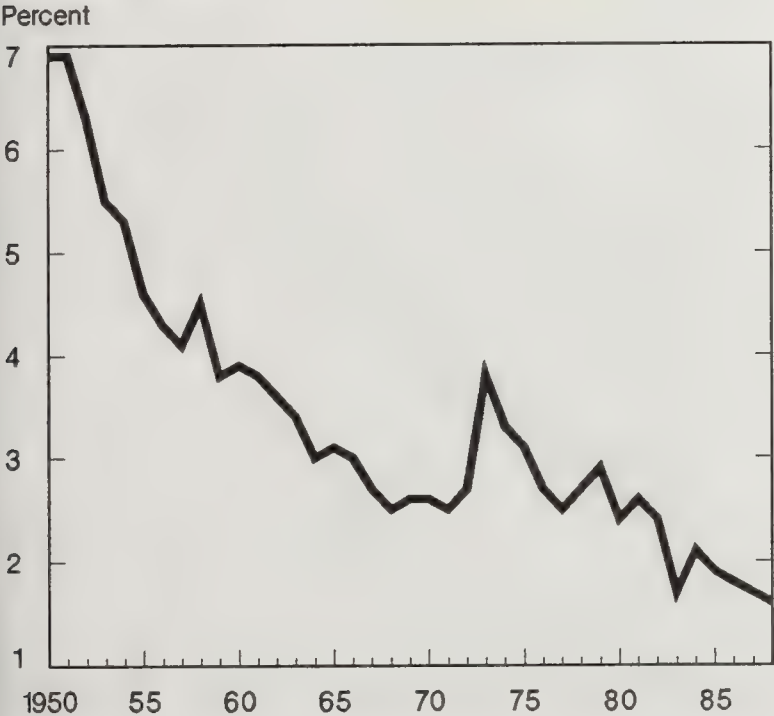


Chart 31
Food and fiber system employment as a percentage of total civilian employment

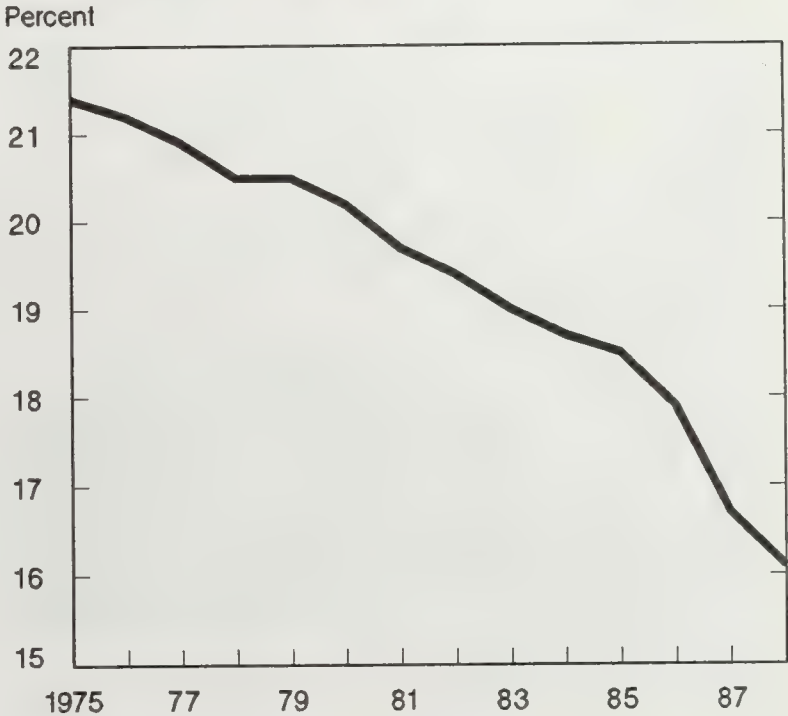
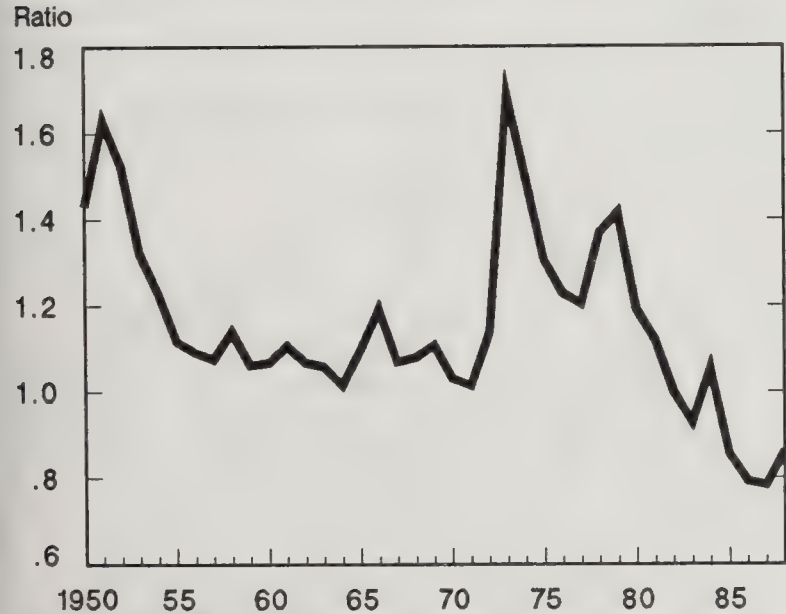
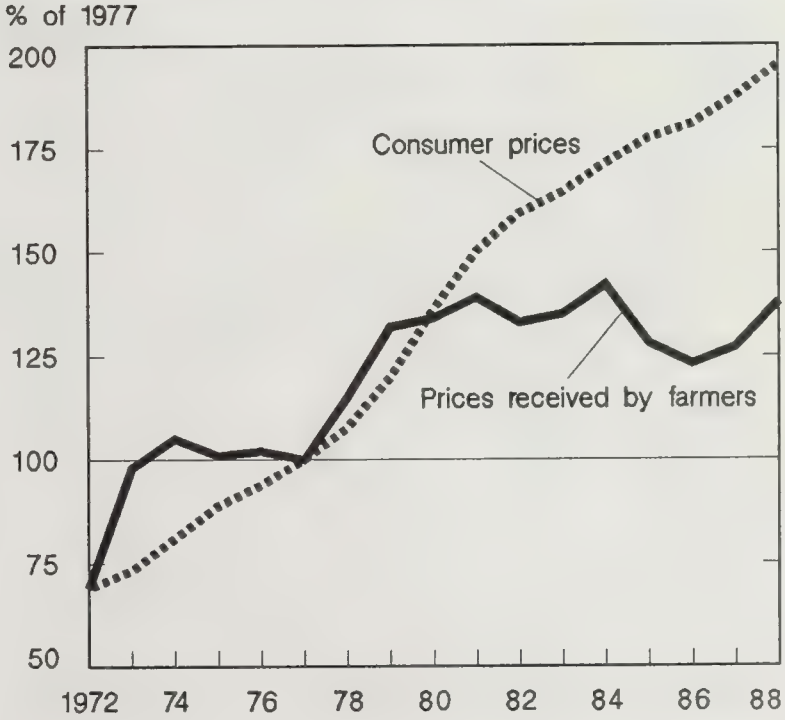


Chart 32
Ratio of implicit price deflators for gross farm product and gross national product



An implicit price deflator measures effect of changes in output and input prices on returns to land, labor, and capital. This ratio signals a continued disinvestment from the farm sector because the nonfarm sector can pay more for available productive factors.

Chart 33
Consumer prices and prices received by farmers



Assets and Finance

With farmers paying down their debt by \$5.2 billion during 1988 and farmland prices improving, farm equity rose for a second consecutive year. Interest rates on farm real estate loans remained favorable in 1988, though real interest rates remained high.

Chart 34
Farm debt

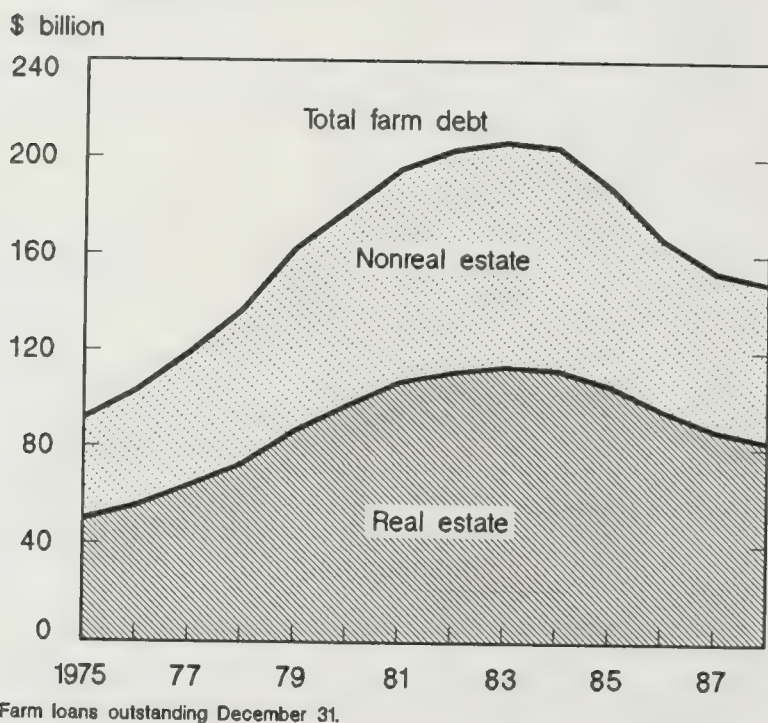


Chart 35
U.S. farm balance sheet

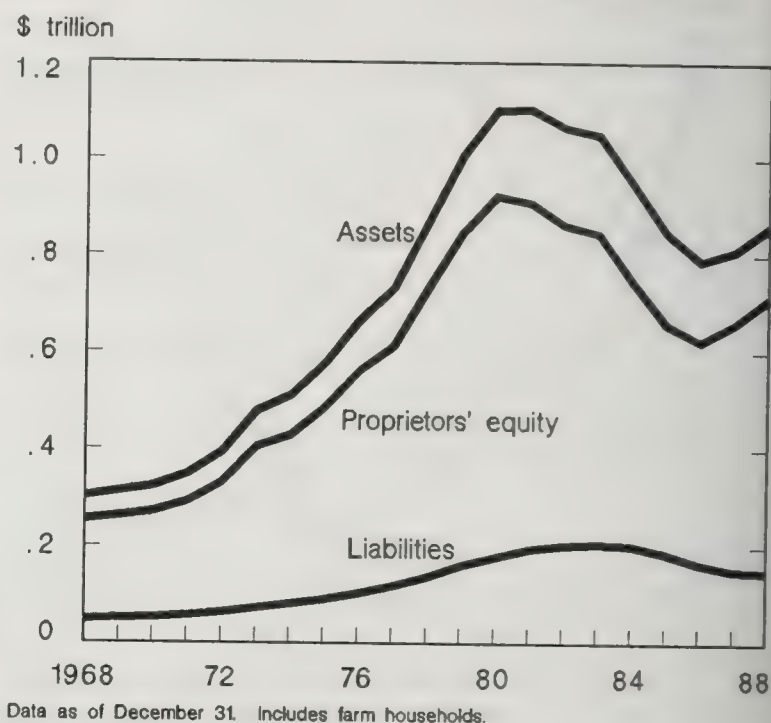
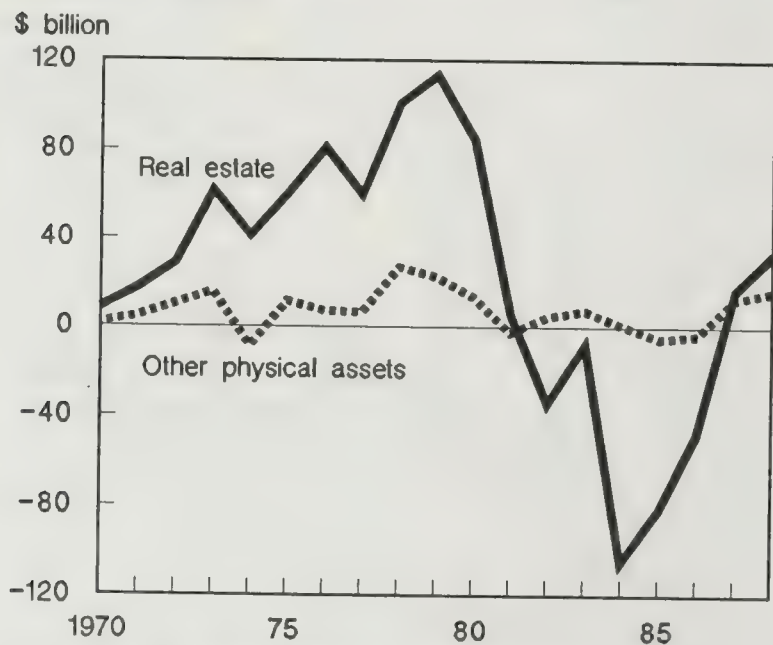
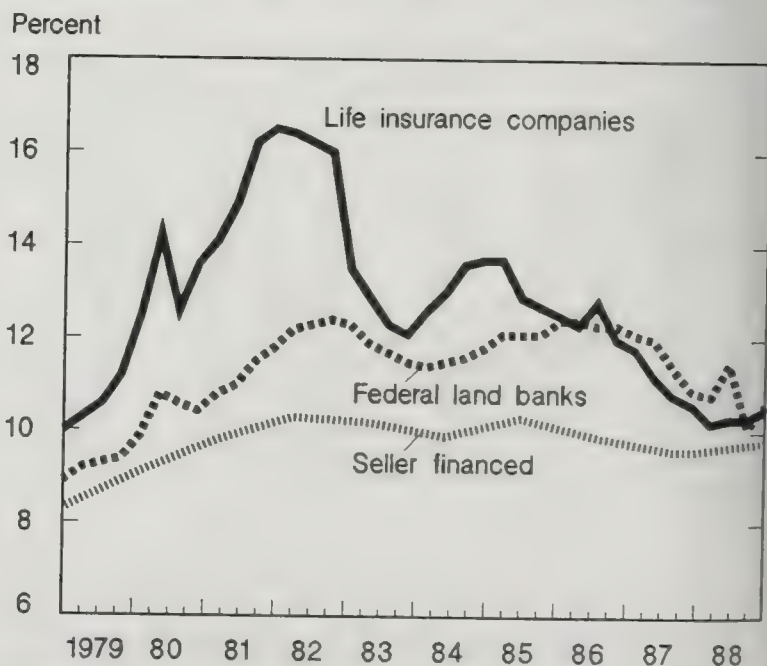


Chart 36
Changes in the value of farm physical assets



Changes in farm real estate values less net capital investments, mostly unrealized. Other physical assets include machinery and motor vehicles, livestock and poultry, and crops stored on farms.

Chart 37
Interest rates on farm real estate loans

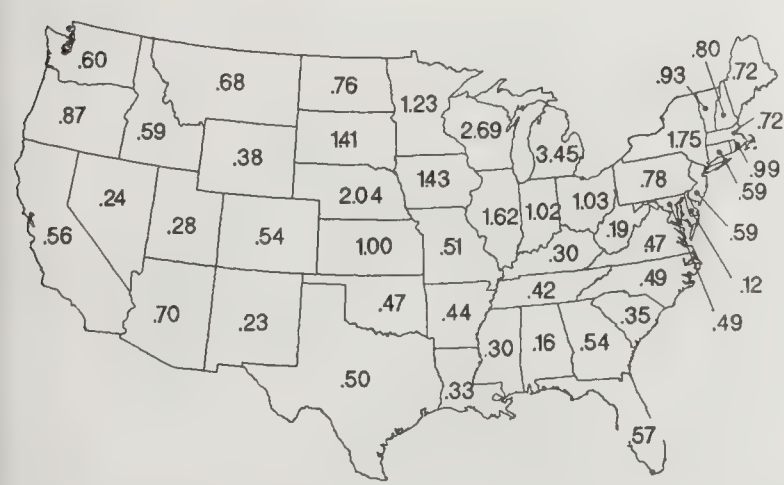


Federal land bank rates exclude new loan fees and charge for the stock borrowers are required to buy.

Finance and Inputs

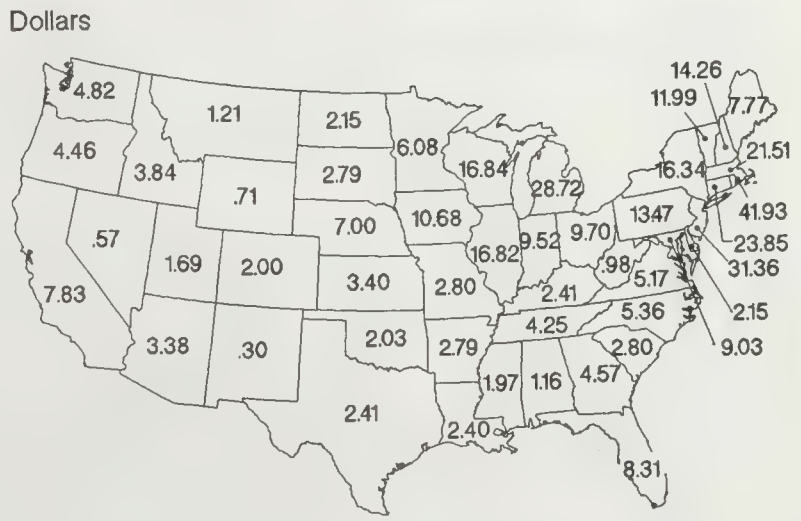
Taxes levied on U.S. farmland and buildings totaled \$4.3 billion in 1987, an 8-percent increase from 1986. The U.S. average tax per acre rose from \$4.60 in 1986 to \$4.97 in 1987. The average tax per \$100 of full-market value rose from \$0.73 in 1986 to \$0.86 in 1987. Drainage investment continues to grow at a fairly constant rate.

Chart 38
U.S. farm real estate taxes, per \$100 of full market value



1987 data, preliminary. Values for Alaska and Hawaii are \$.49 and \$.68. 50-State average, \$.86.

Chart 39
U.S. farm real estate taxes, per acre



1987 data, preliminary. Values for Alaska and Hawaii are \$4.76 and \$10.88. 50-State average, \$4.97.

Chart 40
Drainage Investment and capital in U.S. agriculture

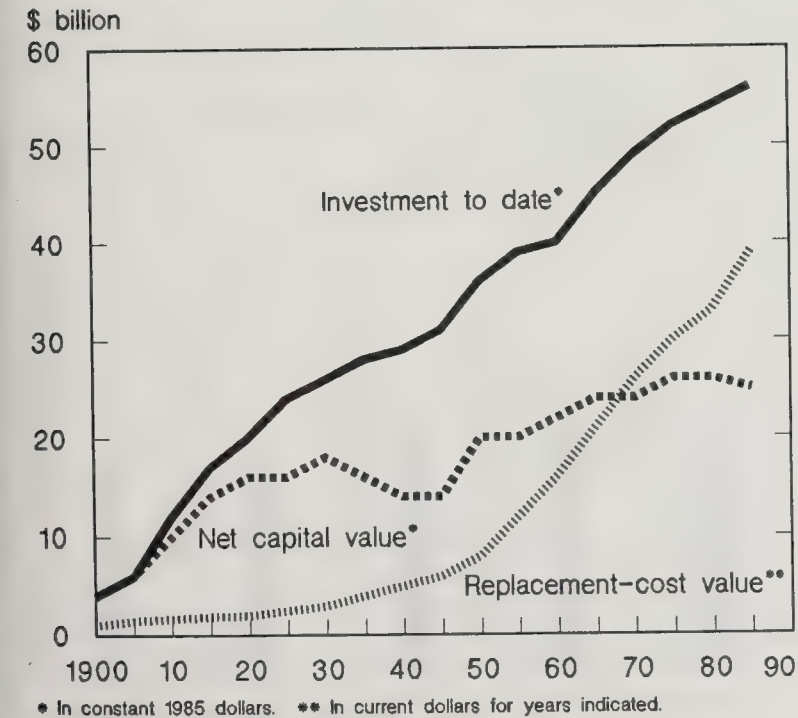
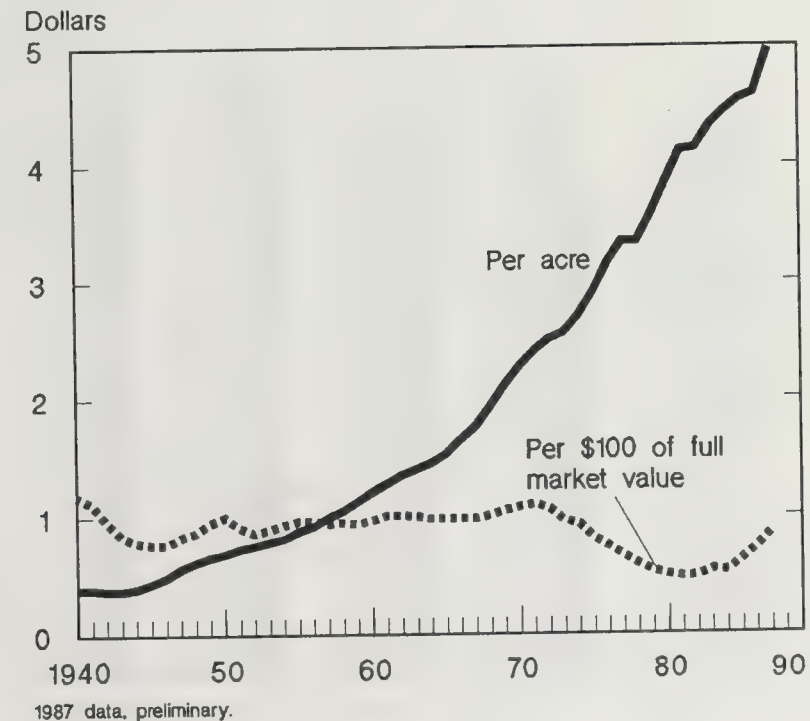


Chart 41
U.S. farm real estate taxes



1987 data, preliminary.

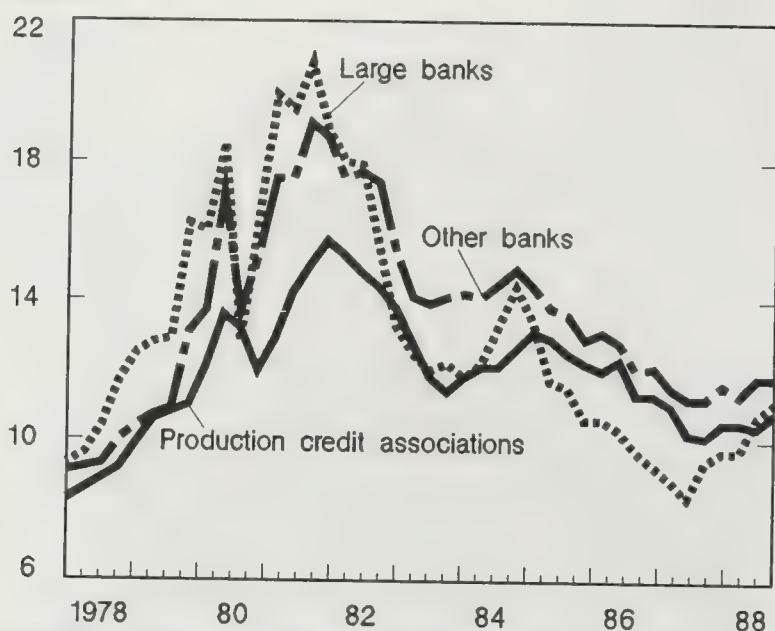
Finance and Inputs

Short-term interest rates increased slightly in 1988, but were still below early 1980's levels. Total farm fuel use declined in 1988 for the 10th consecutive year due to adoption of energy-saving production technologies and a shift from gas to diesel-powered engines. Ninety-five percent of acreage planted to corn, soybeans, and cotton is treated with herbicides.

Chart 42

Interest rates on farm nonreal estate loans

Percent



Rates on new PCA loans include service fees. Bank data are from surveys made by the Federal Reserve System.

Chart 43

Farm fuel use

Billion gallons

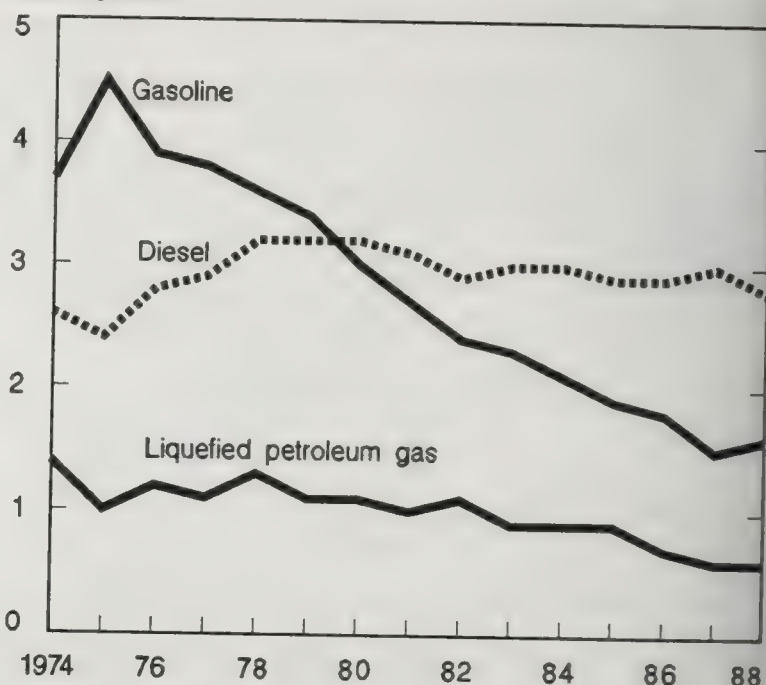
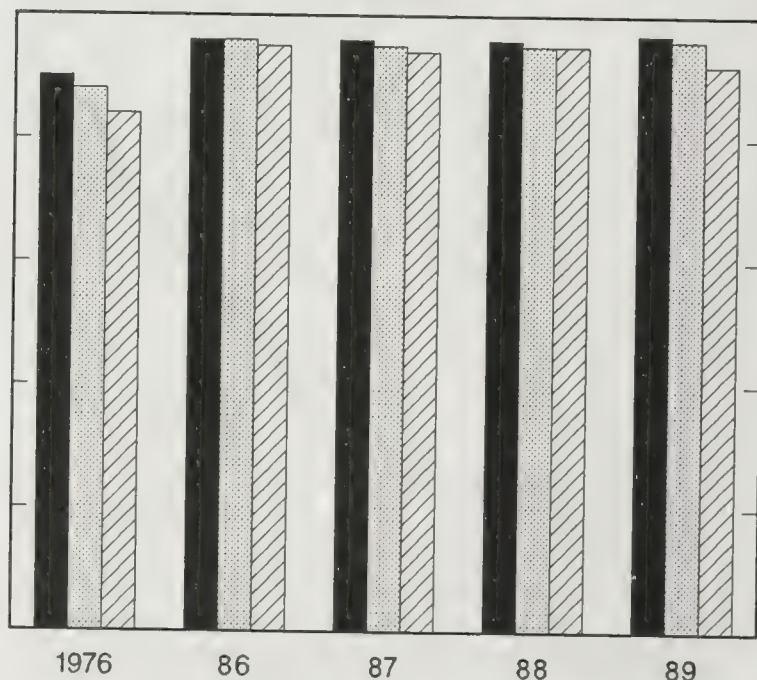


Chart 44

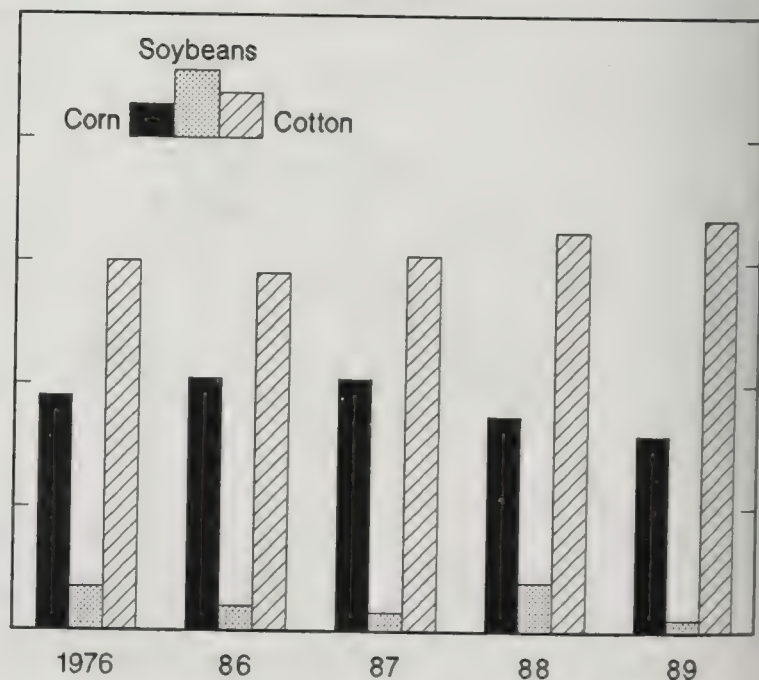
Crop acres treated with pesticides

Herbicides



Percent

Insecticides



Inputs

Fertilizer use rose in 1988 for the first time since 1984, due to stable crop acreage and higher commodity prices. Expenditures for farm machinery rose for the second year in a row despite the drought. Sales of new tractors continued a modest rally begun in 1986, especially for over 40 horsepower two-wheel drive and four-wheel drive tractors.

Chart 45
Farm fertilizer use

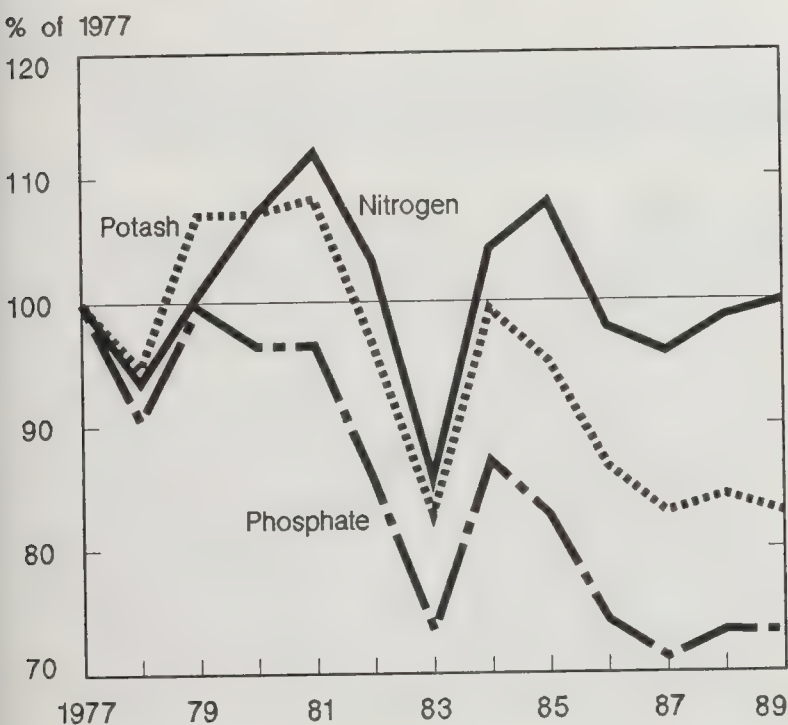


Chart 46
U.S. farm machinery expenditures

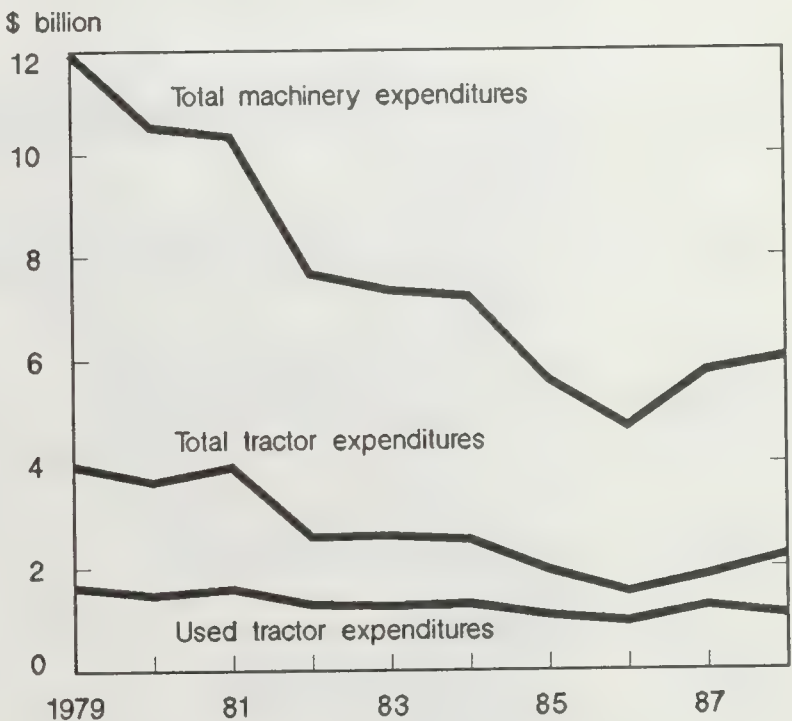


Chart 47
Farm wheel tractor unit sales

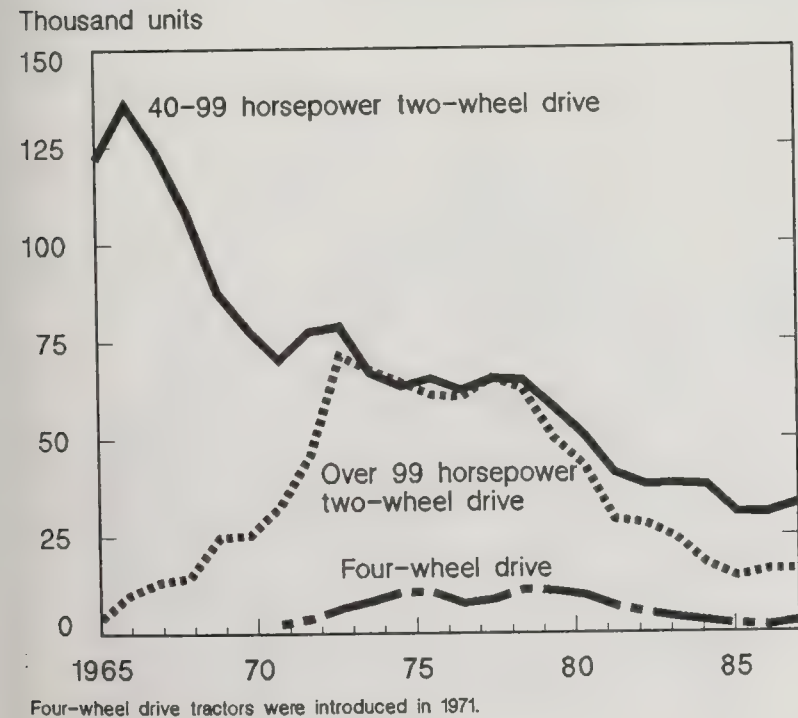
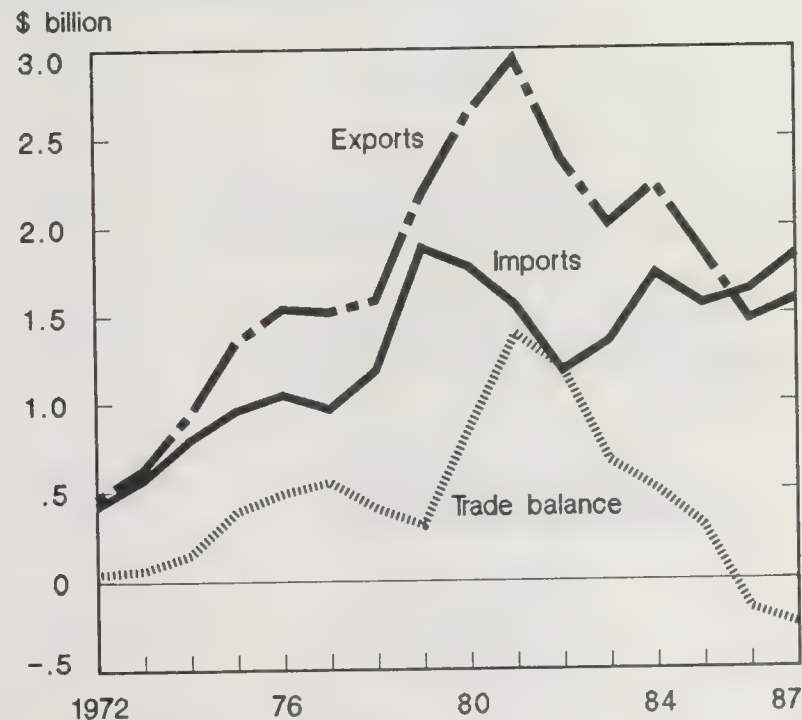


Chart 48
U.S. farm machinery trade

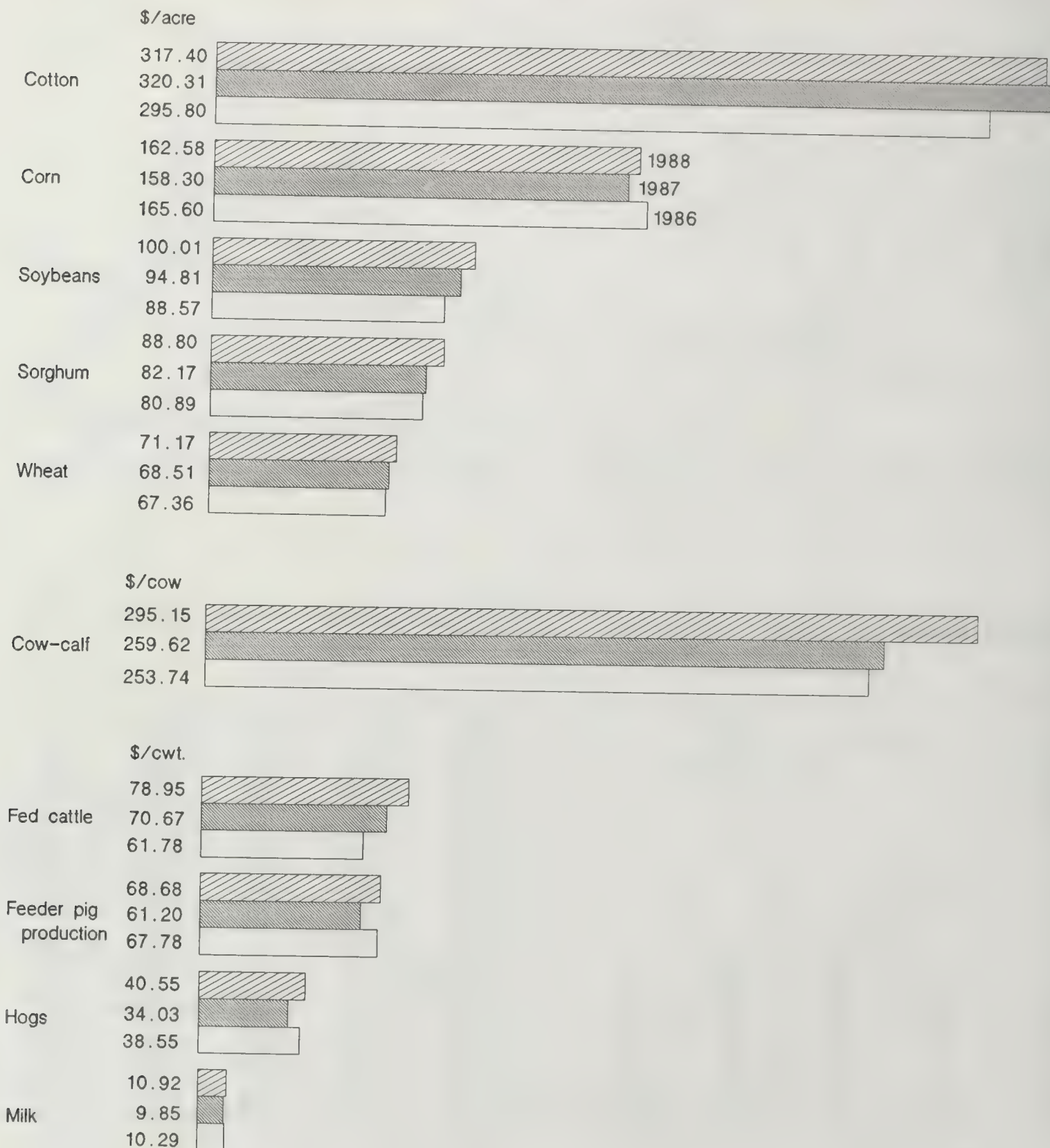


Costs and Returns

Production costs for most major field crops and livestock rose in 1988, because of generally higher prices for fertilizer, feed, and feeder livestock.

Chart 49

Crop and livestock production costs: Cash expenses



Land Use

Cropland acreage harvested increased by 19 million acres, largely due to a decrease in land idled by government programs of 18 million acres. The acreage equivalents of U.S. crops exported continue to increase. Ownership of 5.7 percent of U.S. rural land parcels changed hands in 1988. About 57 percent of that acreage was transferred by voluntary arms-length sales; the remainder by family sales, foreclosure, gift, inheritance, and other methods.

Chart 50
Major cropland uses

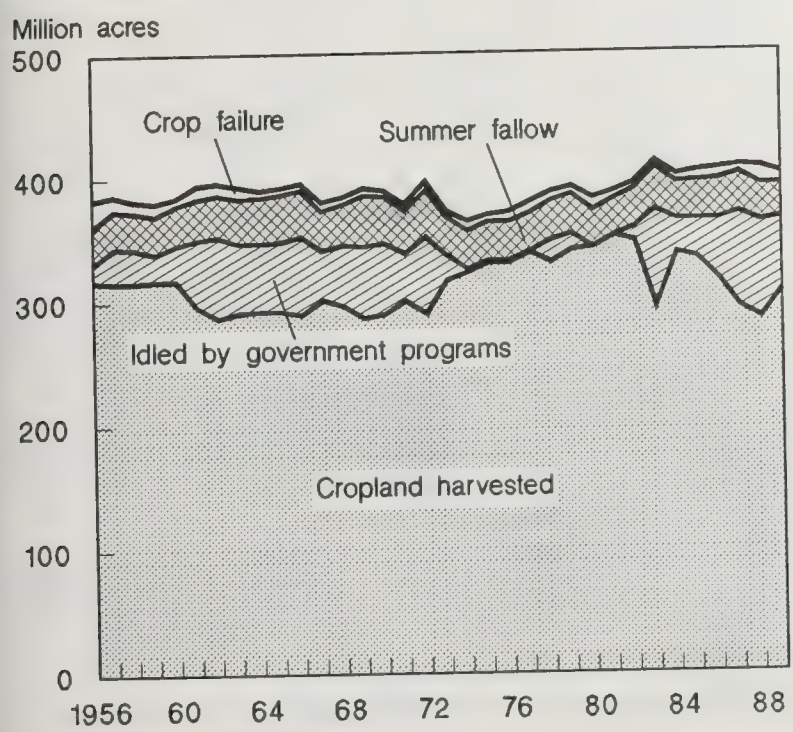


Chart 52
Acreage equivalents of U.S. crops exported

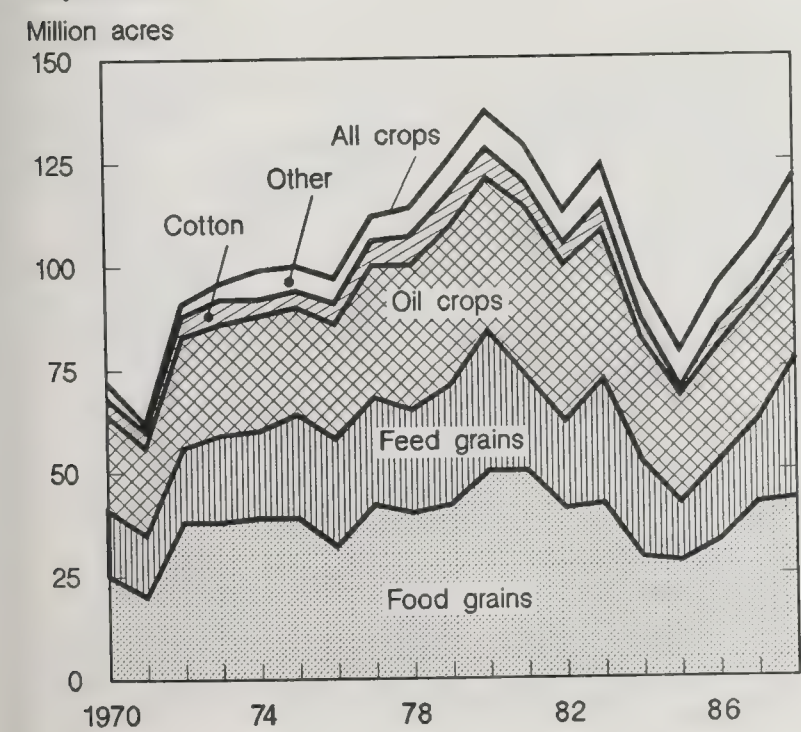
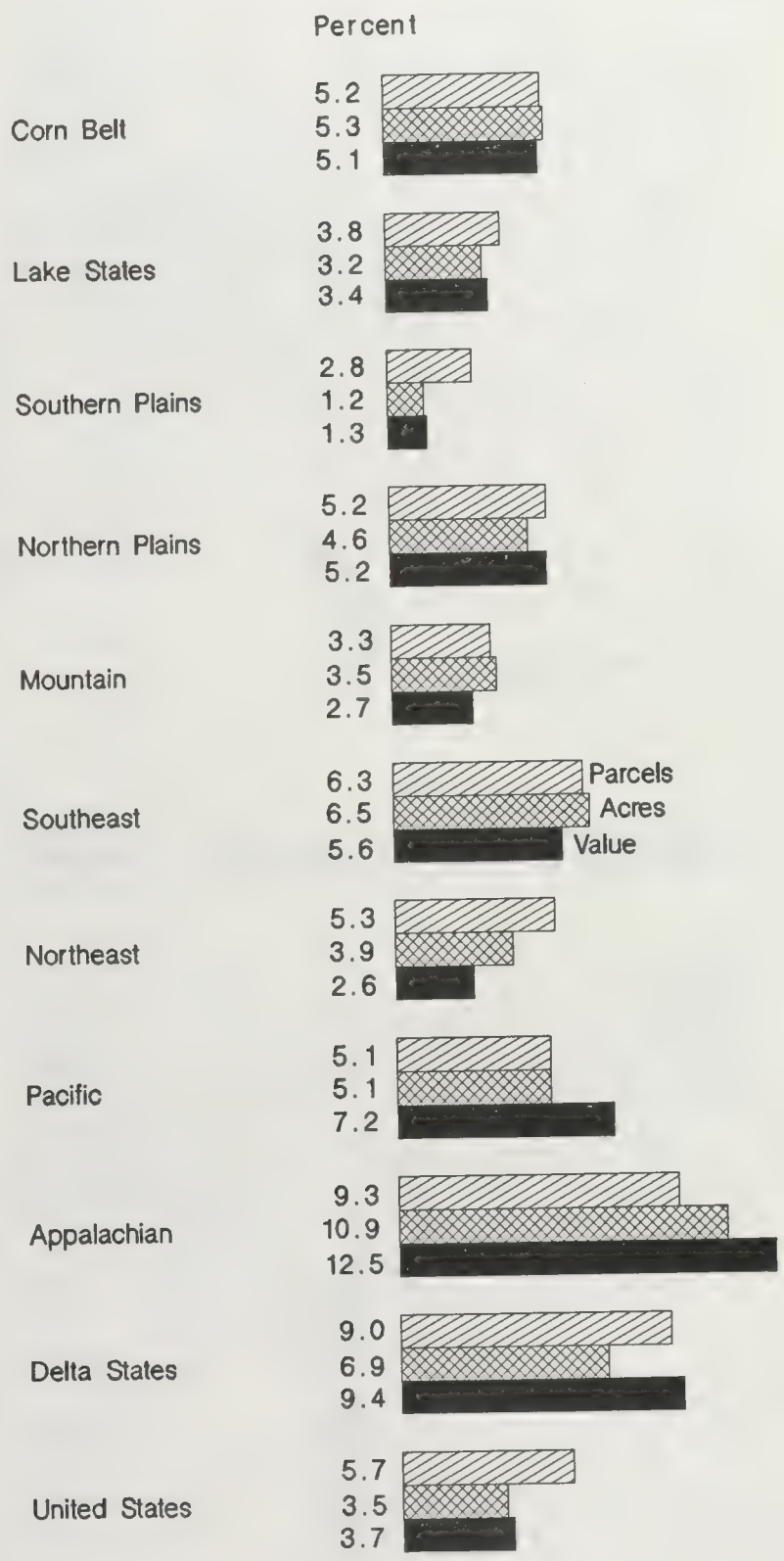


Chart 51
Percent of parcels, acres, and value of rural land transferred in 1988



1989 ERS/NASS survey. Preliminary results.

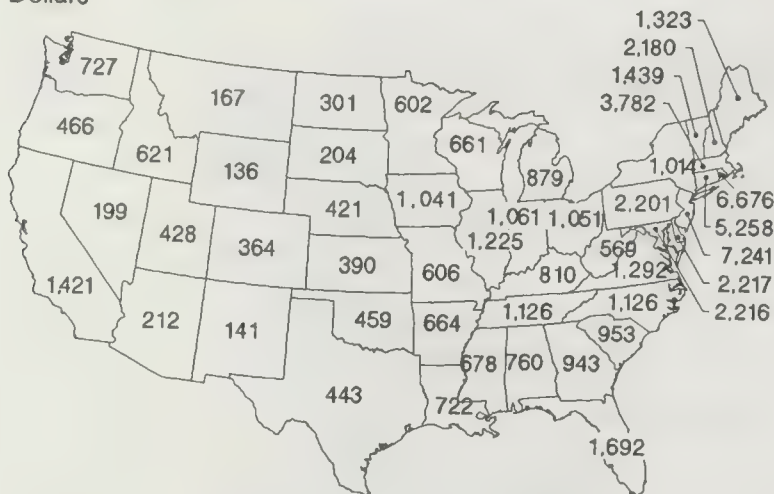
Land Values

Changes in average land values during 1982-89 ranged from a 45-percent increase in the Northeast to a 45-percent decrease in the Lake States. Cash rents for nonirrigated cropland averaged highest in the Corn Belt States, reflecting land earnings. Foreigners owned about 12.5 million acres of U.S. farm and timberland at the end of 1988, or about 0.5 percent of all U.S. land.

Chart 53

Land values per acre

Dollars

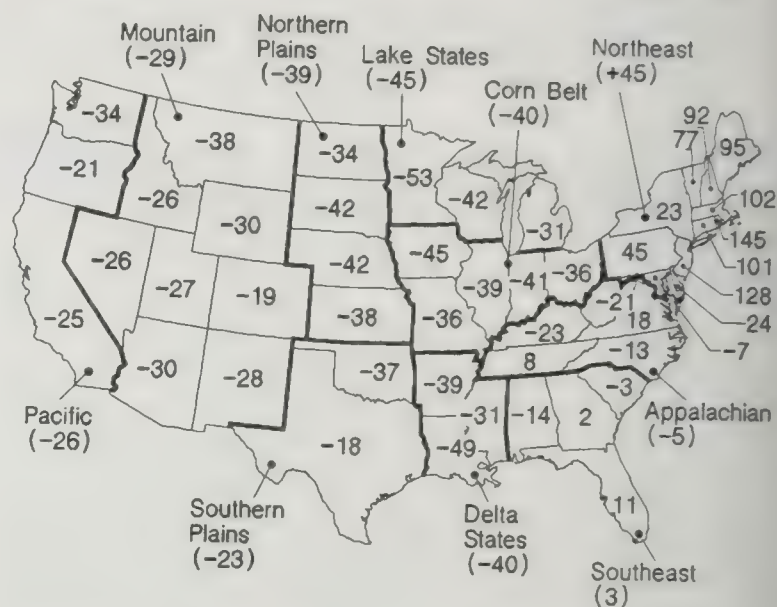


1989 data. 48-State average, 597.

Chart 54

Percentage change in land values, 1982-89

% change

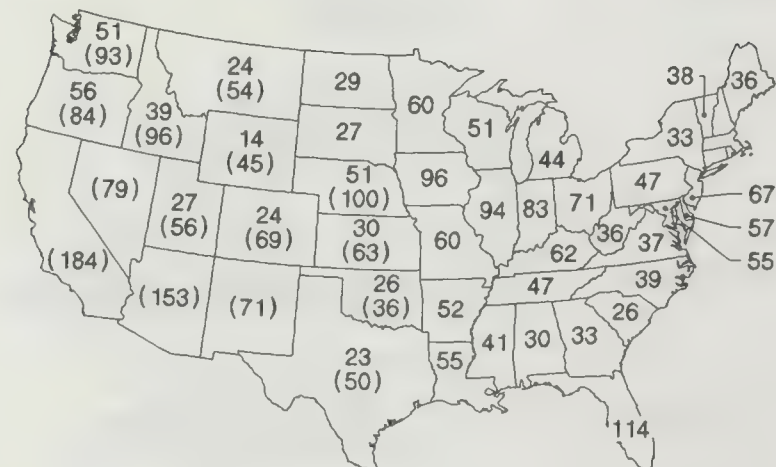


48-State average, -27 percent. Regional averages in parentheses.

Chart 55

Per acre cash rents for cropland

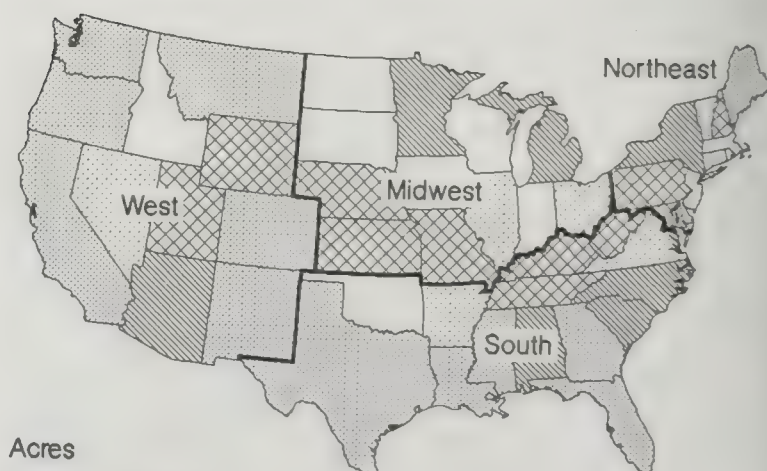
Dollars



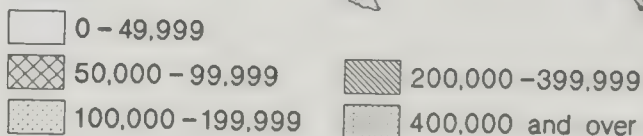
1989 data. Data not available for all States. Rents for irrigated land in parentheses.

Chart 56

Foreign ownership of agricultural land



Acres



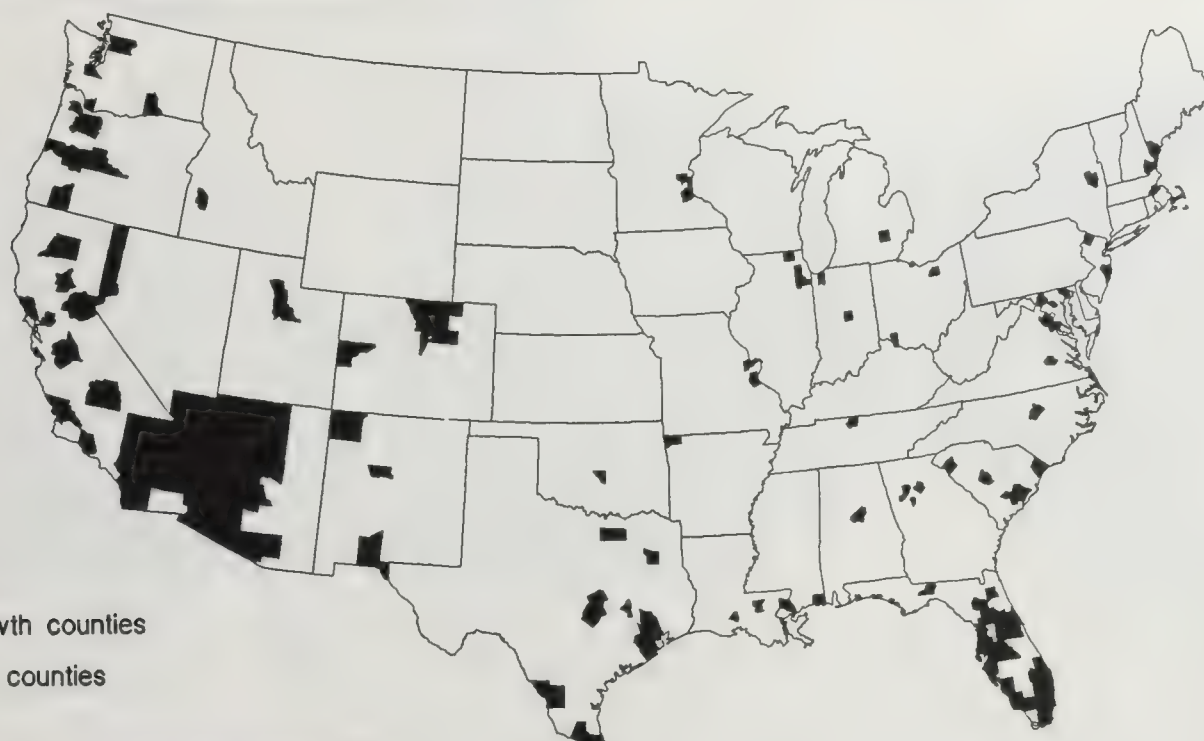
1988 data. Alaska, Guam, and Puerto Rico fall in the 0 - 49,999 category. Hawaii falls in the 50,000 - 99,999 category.

Land Use Changes

In 135 of the fastest growing counties in the United States, residential and other urban land uses increased from 19 to 50 percent from the early 1970's to the early 1980's. Cropland losses were only 2.8 percent. While shifts occurred to and from agriculture, forest, and range, urban uses only absorbed land from the other uses.

Chart 57

Location of fast-growth counties



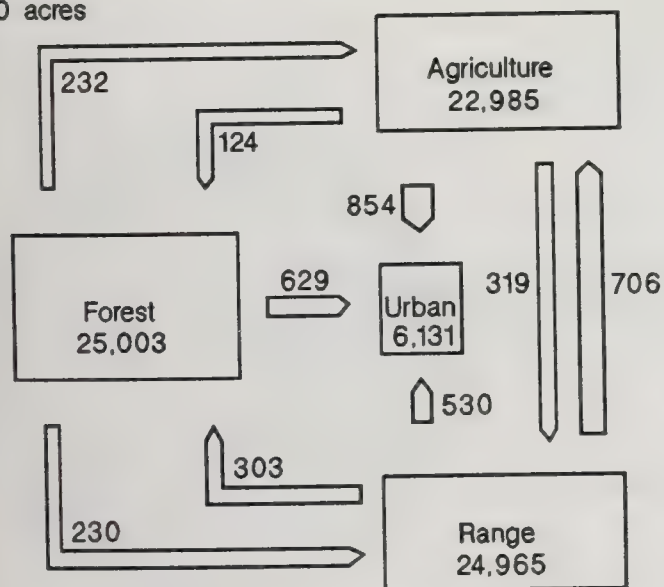
■ Fast-growth counties
□ All other counties

Counties that grew by 25,000 persons and 25 percent, 1970-80.

Chart 58

Shifts in major land uses in fast-growth counties

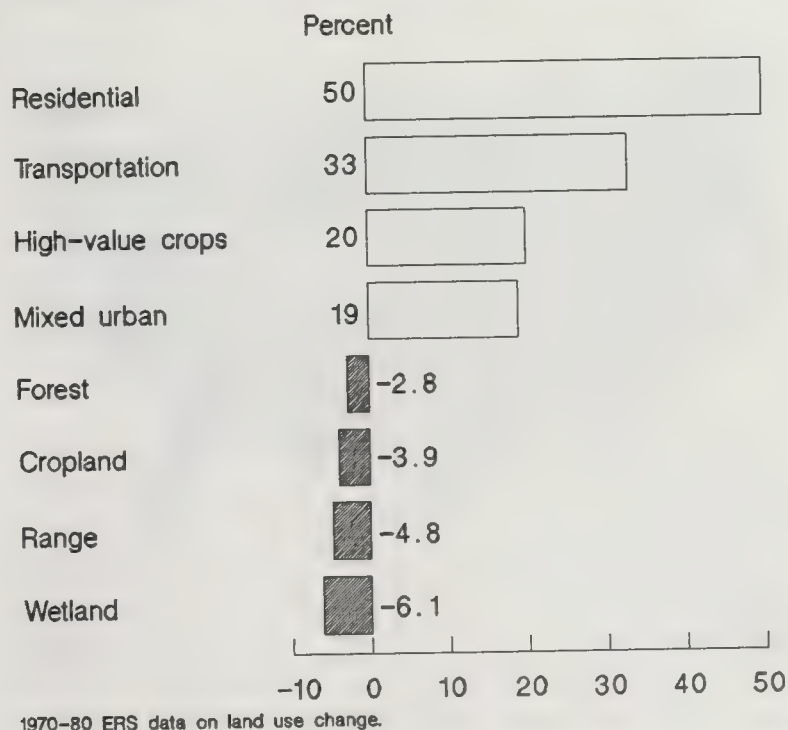
1,000 acres



Cropland and range account for 60% of the urban increase. Very little land is converted back to a resource use once urbanized.

Chart 59

Changes in major land uses in fast-growth counties

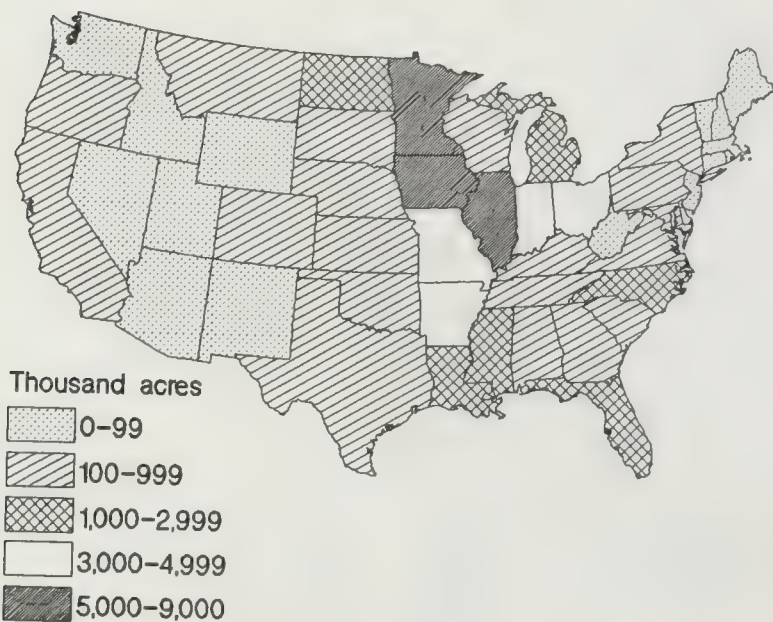


Wetlands

Wetland restoration costs (which are shared between Government and the landowner) stay relatively constant at \$115-\$152 per acre as reserve size increases. Average easement costs (borne solely by the Federal Government) rise from \$135-\$515 per acre as reserve size increases. About 65 million acres of existing wetlands remained in private ownership in 1982, much of that on farms. Conversion to agriculture accounted for 87 percent of the 12.2 million wetland acres lost between the mid-1950's and mid-1970's.

Chart 60

Cropland on former wetland soils, 1982

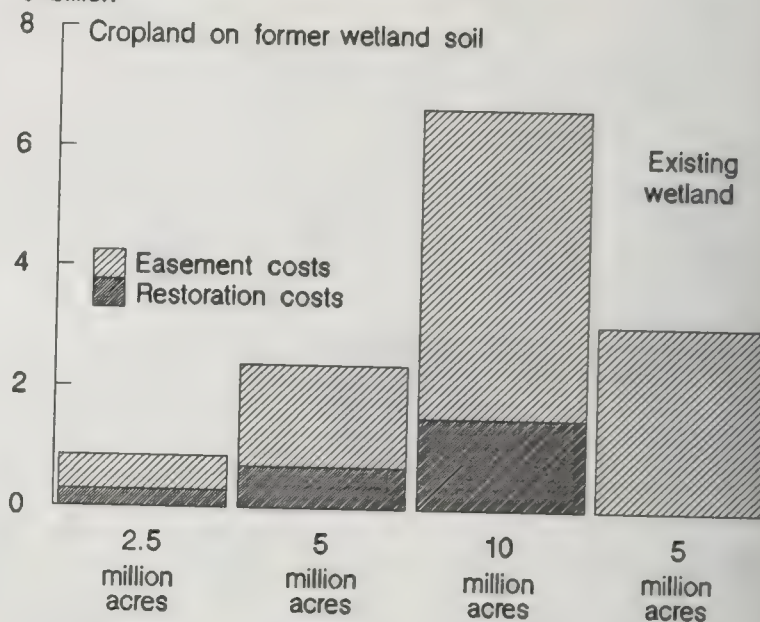


Nonfederal rural land, National Resources Inventory.

Chart 61

Costs of an agricultural wetland reserve, existing and former wetland

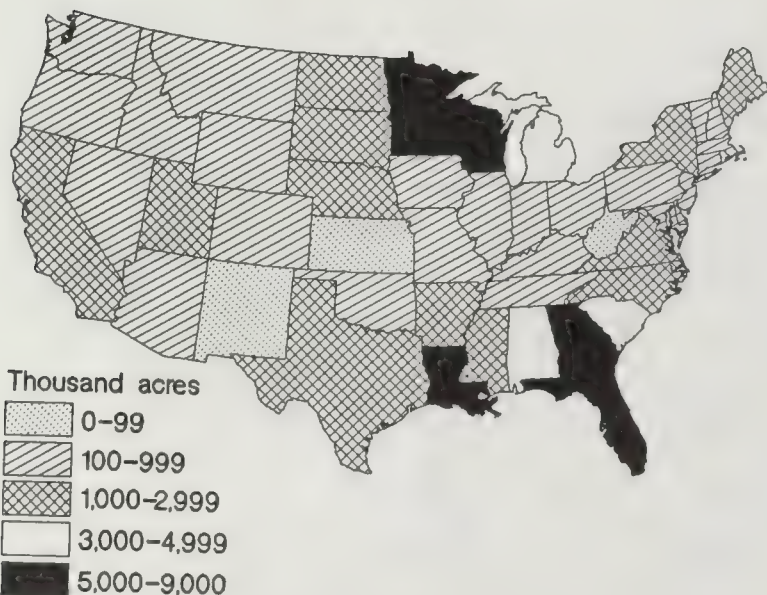
\$ billion



1990 data, estimated.

Chart 62

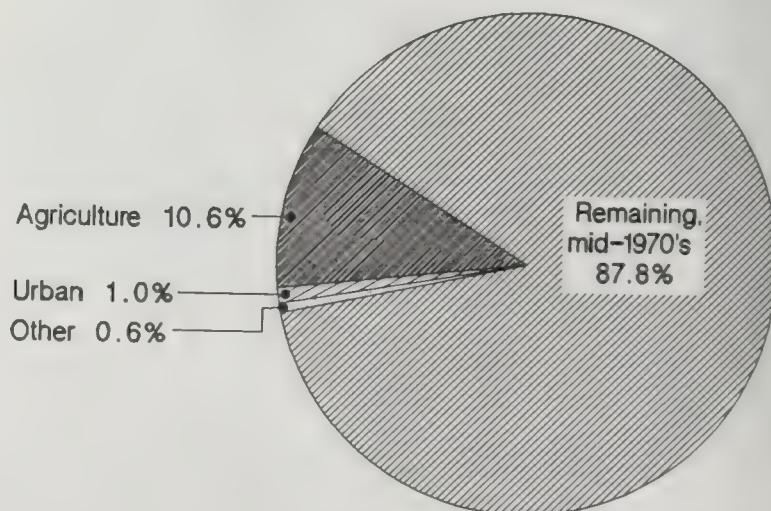
Remaining wetlands, 1982



Nonfederal rural land, National Resources Inventory.

Chart 63

Wetland losses, United States: Mid-1950's to mid-1970's

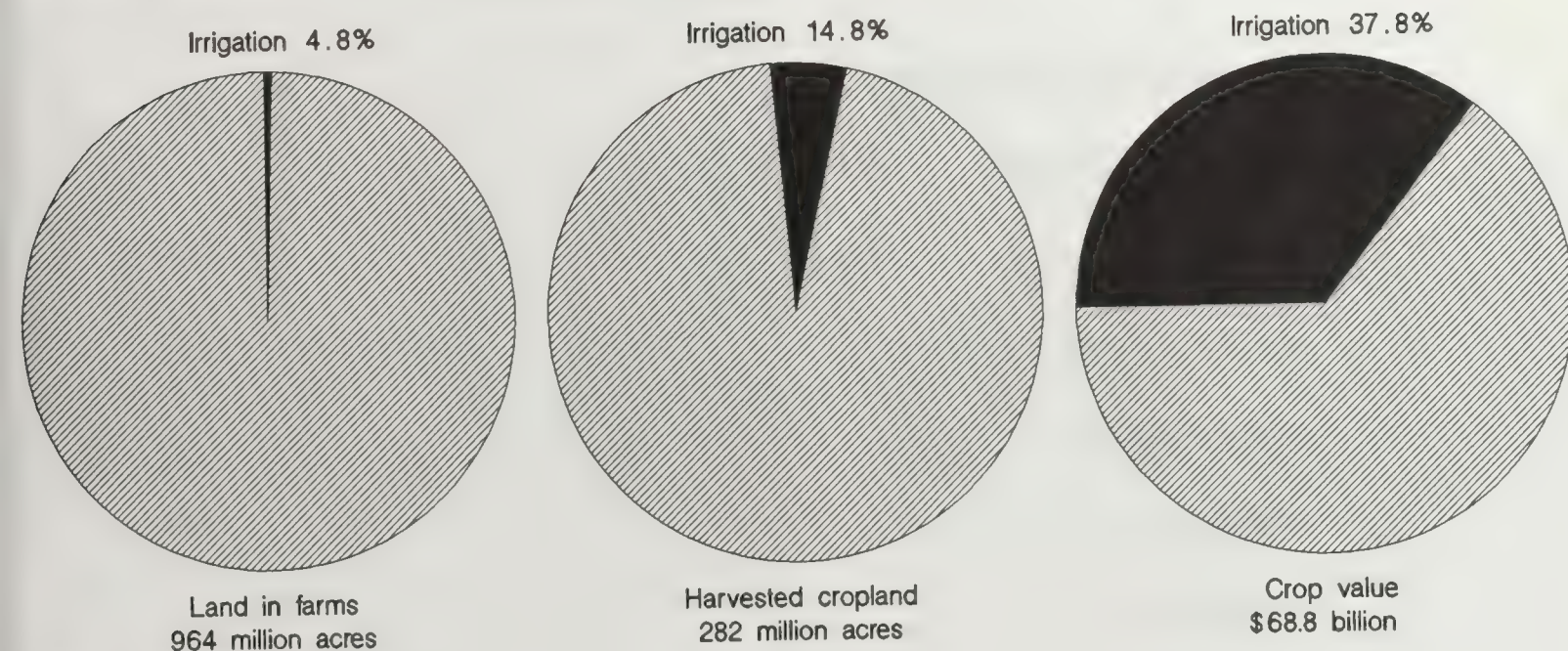


The pie represents 108 million acres of wetland existing in the mid-1950's.

Irrigation

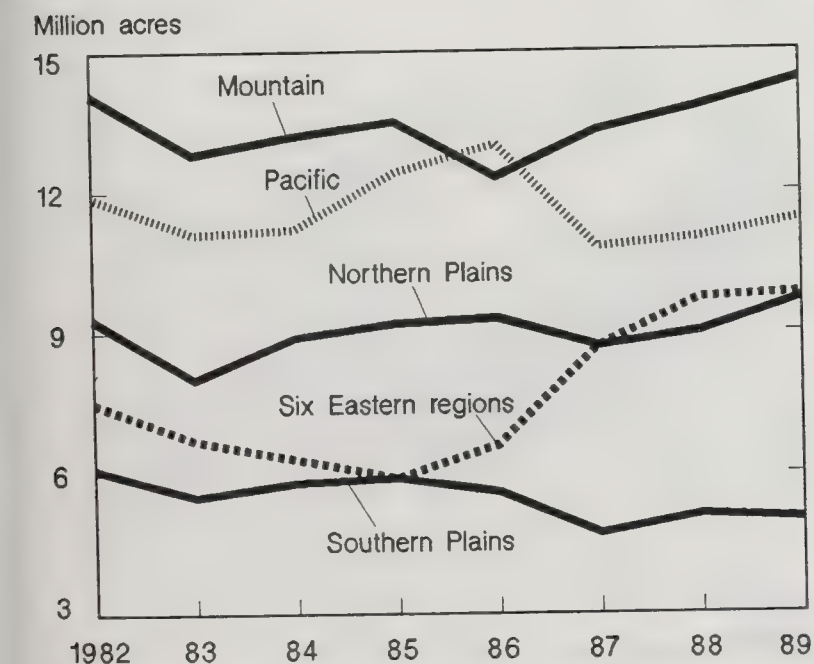
Irrigated crops accounted for \$26 billion of total crop value. Irrigated acres by region vary annually due to changes in crop and input prices, commodity programs, climatic factors, and technology adoption. The West and South are much more dependent upon irrigation than other parts of the United States.

Chart 64
Irrigation and farm production



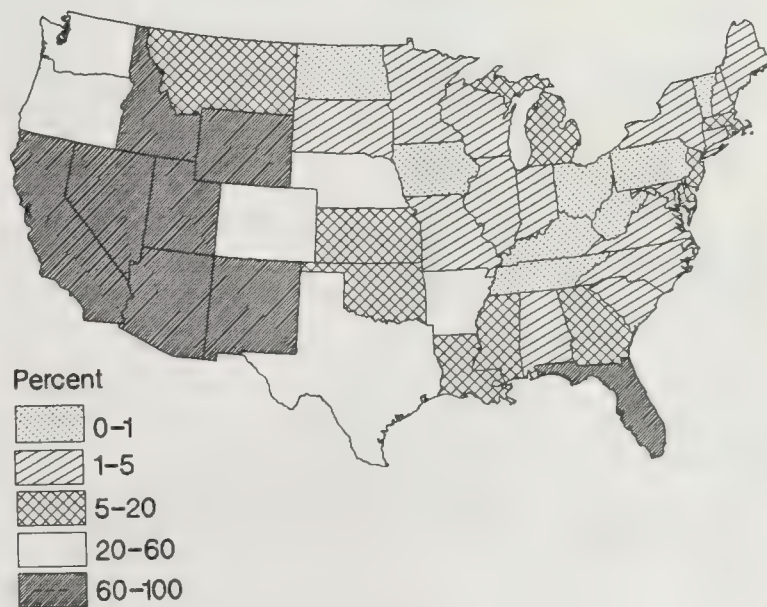
1987 data. Source: Census of Agriculture.

Chart 65
Irrigated acres by production region



Data for 1982 and 1987 are from the Census of Agriculture. Data for other years are ERS-USDA estimates.

Chart 66
Irrigated harvested cropland as a percent of total harvested cropland



1987 data. Source: Census of Agriculture

Irrigation

The percentage of harvested cropland irrigated varies by crop. Differences can be due to geographic concentration of production and variations in cultural practices. The Midwest and South rely most heavily on groundwater for irrigation. Nearly all declines in irrigated acreage between 1982 and 1987 occurred in the Western States.

Chart 67

Percent of harvested cropland irrigated

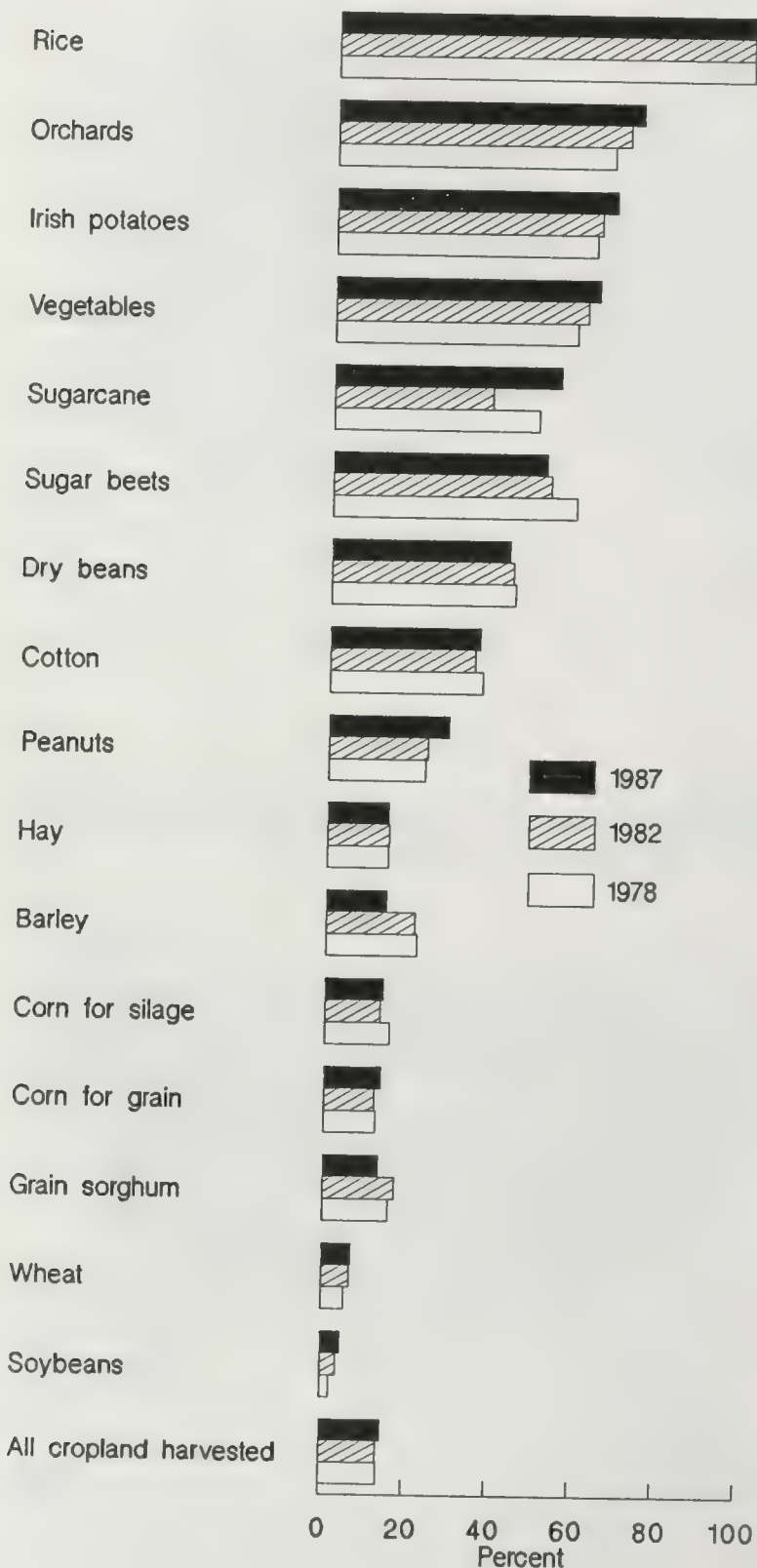
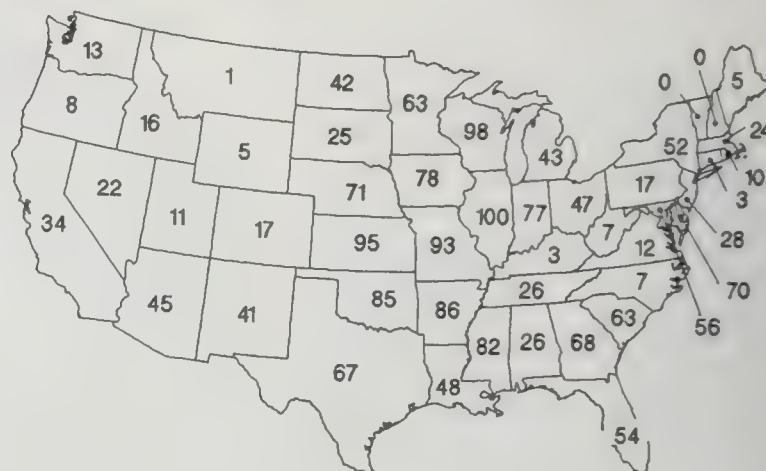


Chart 68

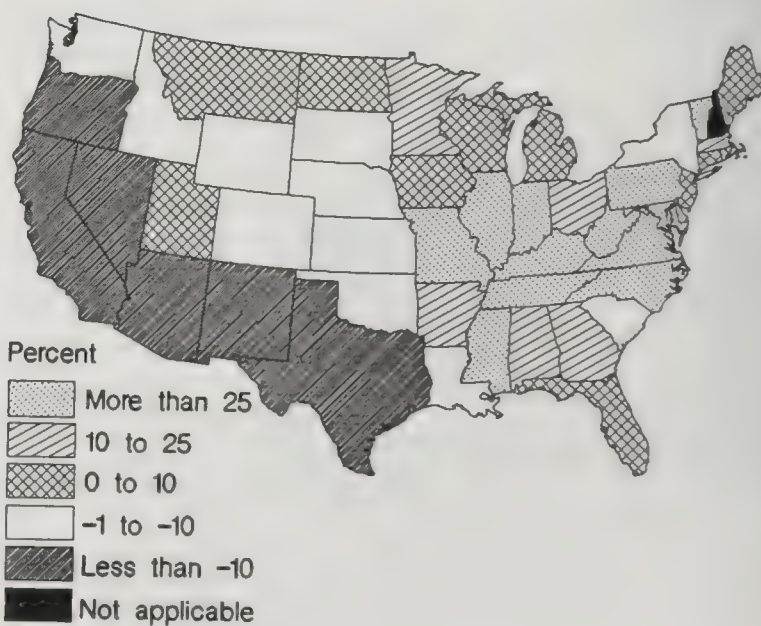
Percent of irrigation water from groundwater sources



1985 data. Source: U.S. Geological Survey

Chart 69

Change in irrigated acres, 1982-87



Source: Census of Agriculture.

Timber Products

U.S. production of timber products rose in 1988 and exports rose to record levels. Consumption and imports declined for the first time since 1985. Imports supplied a little over 23 percent of total consumption in 1988. About 18 percent of total production was exported.

Chart 70
Timber products production

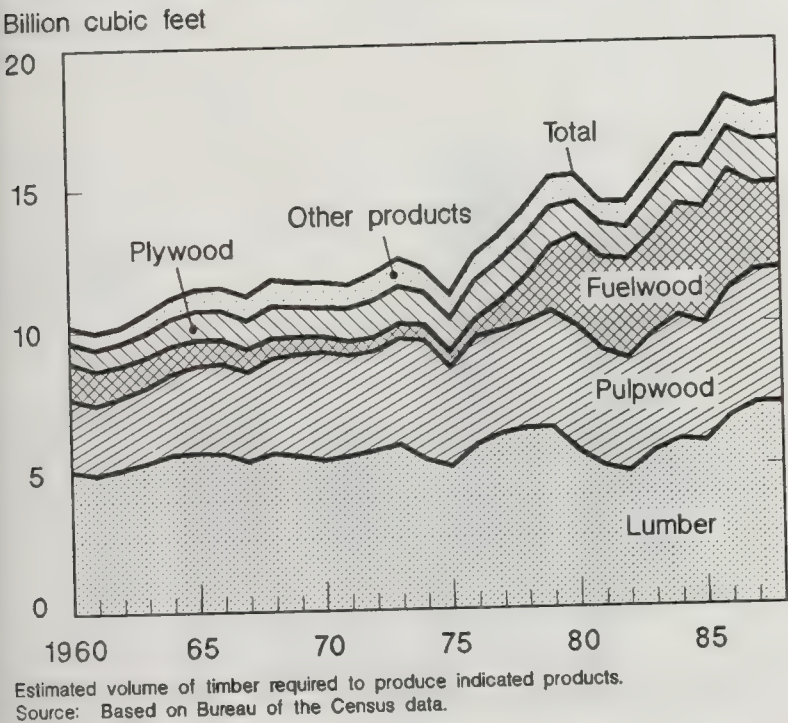


Chart 71
Timber products consumption

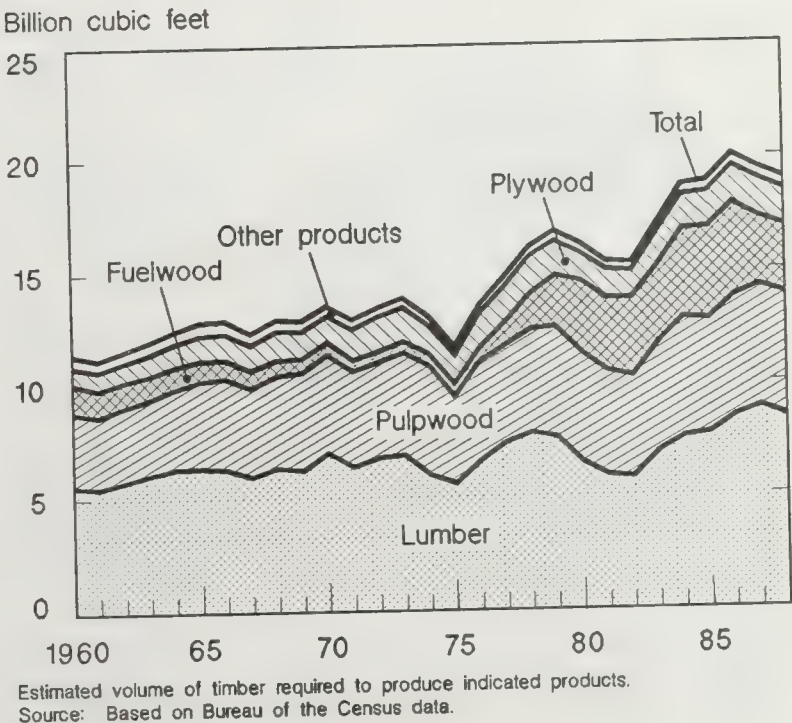


Chart 72
Timber products imports

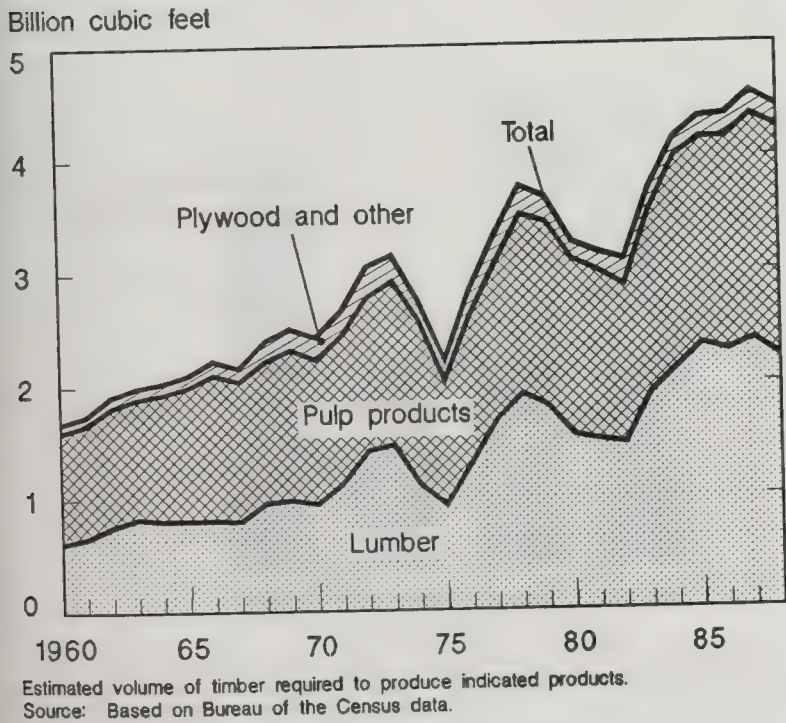
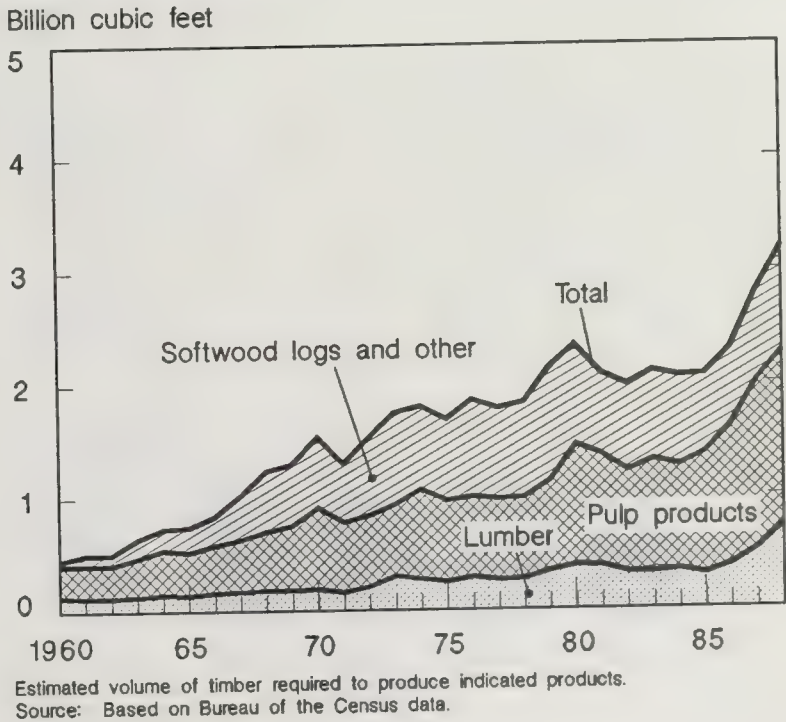


Chart 73
Timber products exports



Forests and Timber

Forests occupy approximately a third of the Nation's total land area. Two-thirds of the forest area is timberland, or productive forests, owned by the public, forest industries, farmers, and other individuals and firms. In total, U.S. timberland contains 830 billion cubic feet of timber, 57 percent softwood species and 43 percent hardwoods.

Chart 74

Forest land areas of the United States

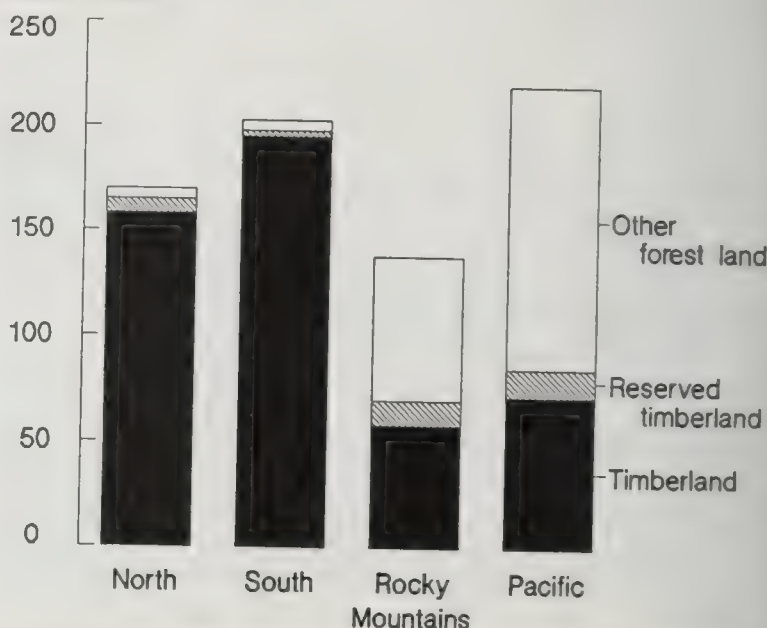


1987 data. Hawaii and Alaska included in Pacific Coast.

Chart 75

Forest land areas of the United States, by type, 1987

Million acres



Timberland is forest land capable of producing 20 cubic feet per acre of industrial wood annually and not reserved from harvests.

Chart 76

Timberland ownership in the United States, 1987

Million acres

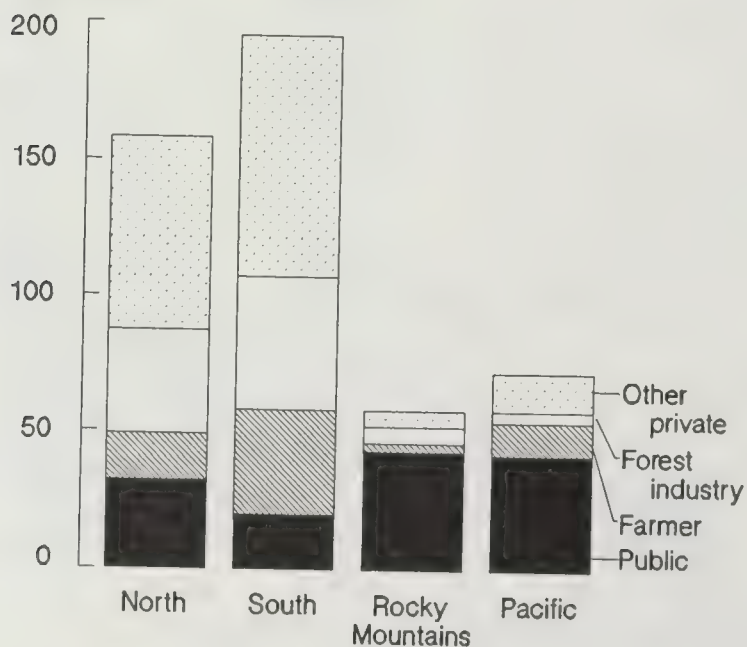
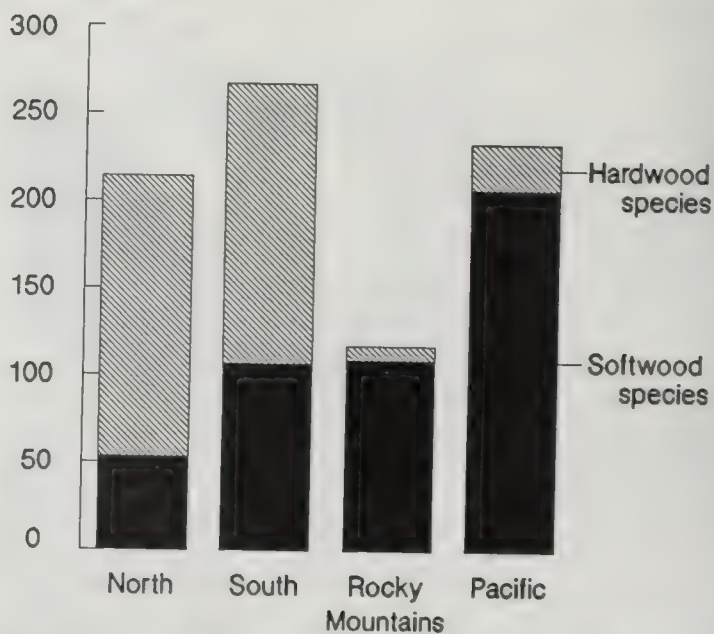


Chart 77

Volume of timber on timberland in the United States, 1987

Billion cubic feet



Net volume, which is gross volume less deductions for rot, roughness, and poor form.

Conservation

USDA and related State and local conservation program expenditures exceeded \$3.2 billion in 1989. Over 60 percent of total USDA conservation expenditures are related to the Conservation Reserve Program (CRP). The Corn Belt and Northern Plains account for nearly 60 percent of all conservation-tilled acres. Almost 90 percent of the acres with conservation tillage produced corn, soybeans, or small grain in 1989.

Chart 78
USDA and related State and local program conservation expenditures

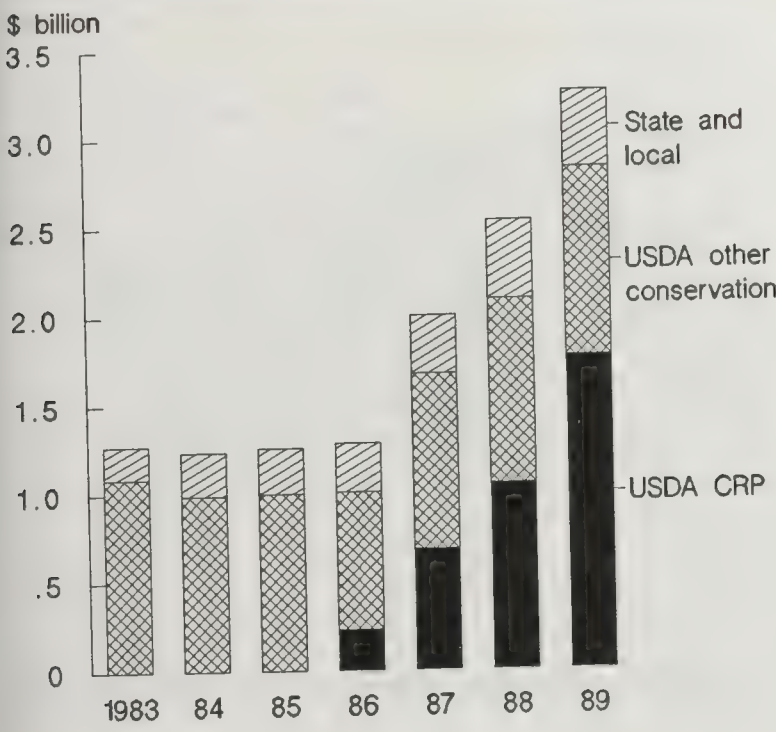


Chart 79
USDA conservation expenditures, 1989

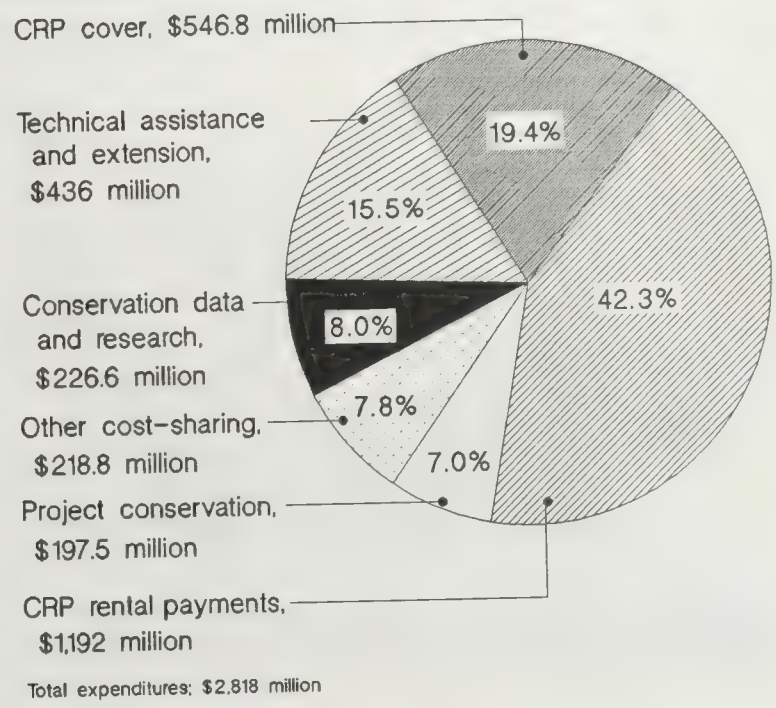


Chart 80
Tillage practices on acres planted, by region

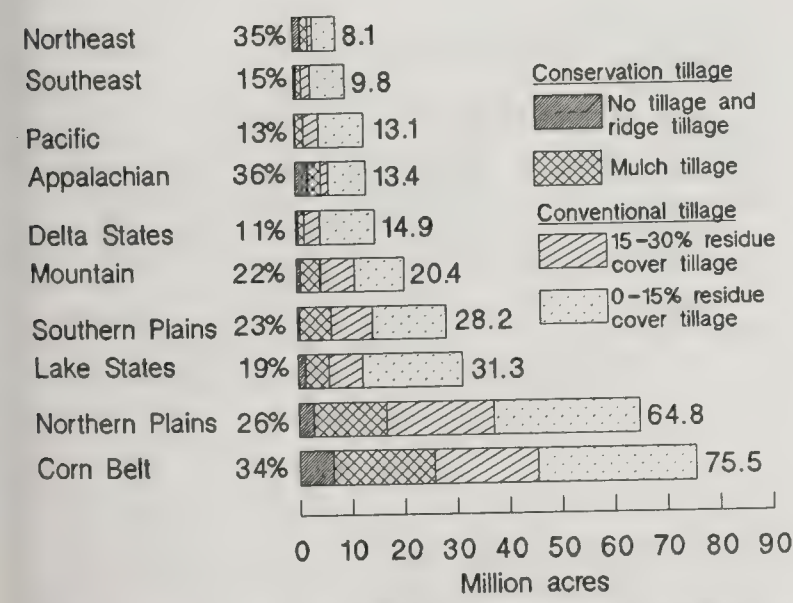
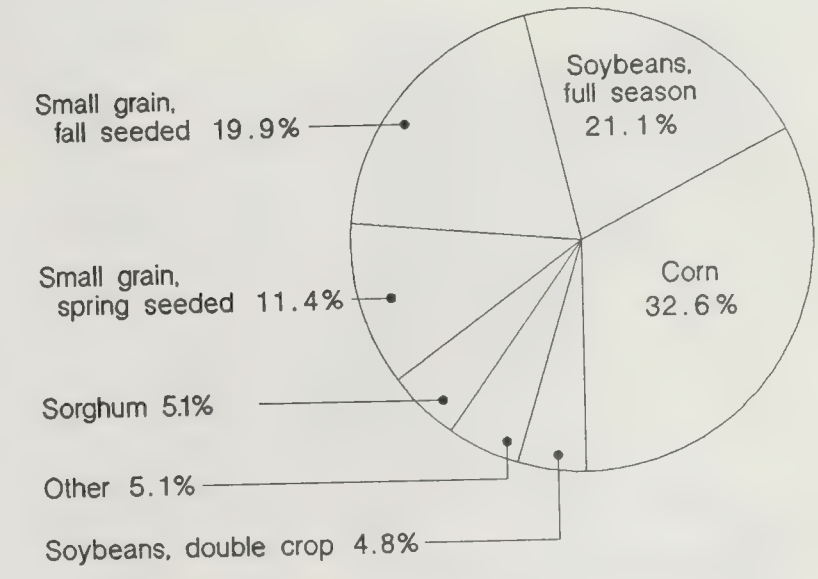


Chart 81
Total acres planted with conservation tillage by crop, 1989



1989 data. Source: Conservation Technology Information Center. Percentages show total regional conservation tillage use as a percent of acres planted in the region. Numbers show total acres planted in the region.

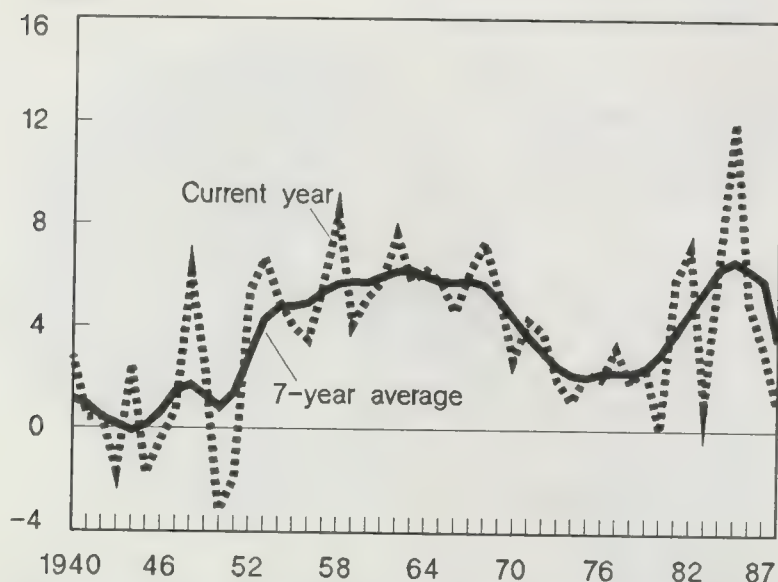
Conservation

Excess production capacity peaked in 1986 and continues to decline. Conservation Reserve Program enrollment is approaching the 40-45 million acre goal. Enrollment is concentrated in the Plains and Mountain States, with lowest participation in the Northeast.

Chart 82

Excess production capacity in 12 commodities

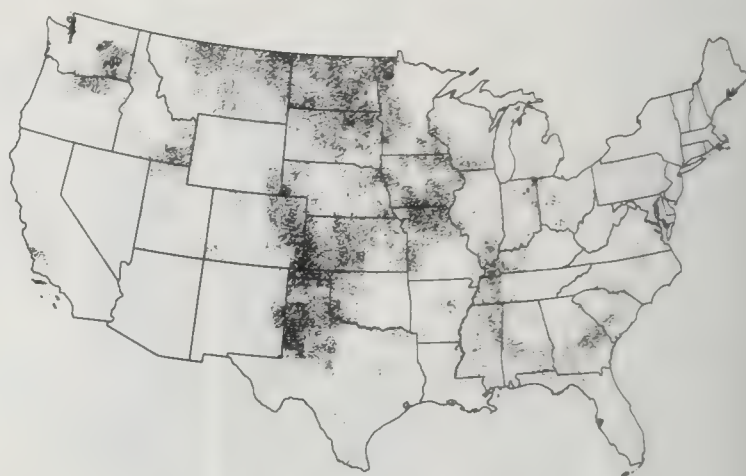
Percent



Percentage of total U.S. production of wheat, corn, oats, barley, rye, sorghum, cotton, soybeans, rice, tobacco, peanuts, and dairy products. Excess production capacity is the difference between potential output and commercial demand at prevailing farm prices.

Chart 83

Total acreage enrolled in the Conservation Reserve Program as of February 1989



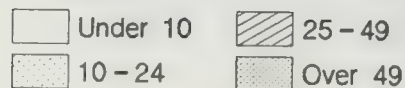
One dot equals 1,000 acres. Total enrollment through the eighth signup, 30.6 million acres.

Chart 84

Conservation reserve acreage as a percentage of eligible cropland



Percent



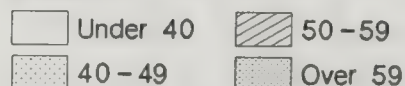
1989 data.

Chart 85

Average annual per acre rental payment of conservation reserve lands by State



Dollars



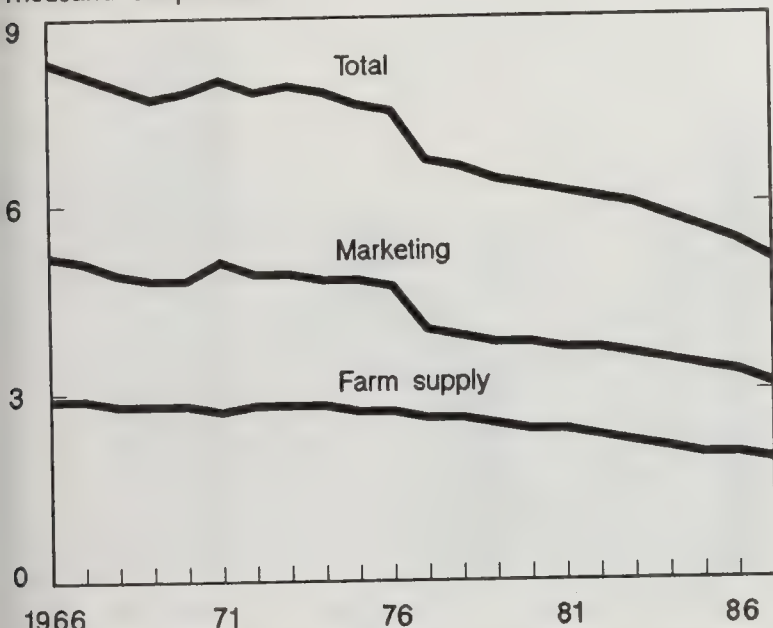
1989 data.

Farmer Cooperatives

The decrease in number of U.S. farmer cooperatives in 1987 reflects a continuing trend of merger, consolidation, acquisition, and dissolution. The long-term decline in memberships reflects in part the decreasing number of U.S. farms and farmers. Farmer cooperative total assets increased in 1987 by 4.8 percent.

Chart 86
Farmer cooperatives in the United States

Thousand cooperatives

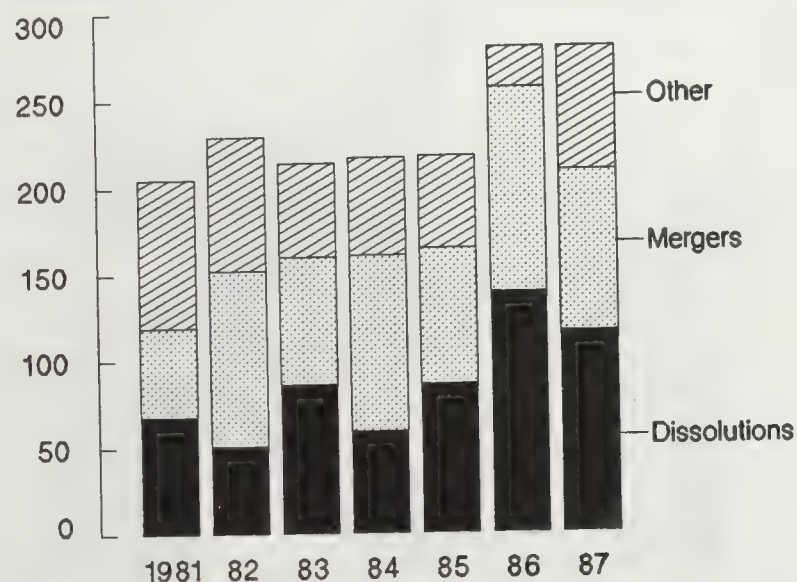


Total includes a small number of cooperatives that provide specialized related services.

Chart 87

Mergers and dissolution of U.S. farmer cooperatives

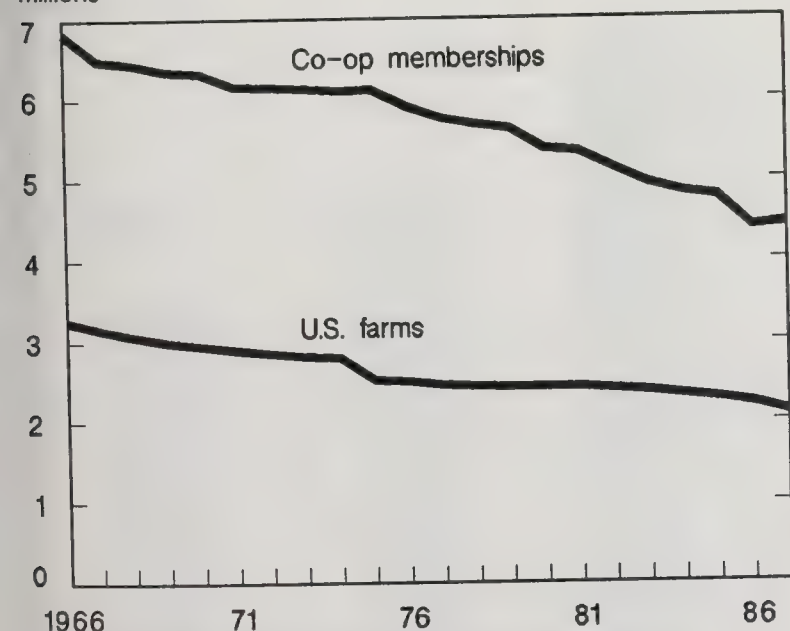
Number



Based on a list of all U.S. farmer cooperatives maintained by the Agricultural Cooperative Service. Mergers also include acquisitions and consolidations. Other includes cooperatives dropped due to inactivity, reassignment, and miscellaneous reasons.

Chart 88
U.S. farms and farmer cooperative memberships

Millions

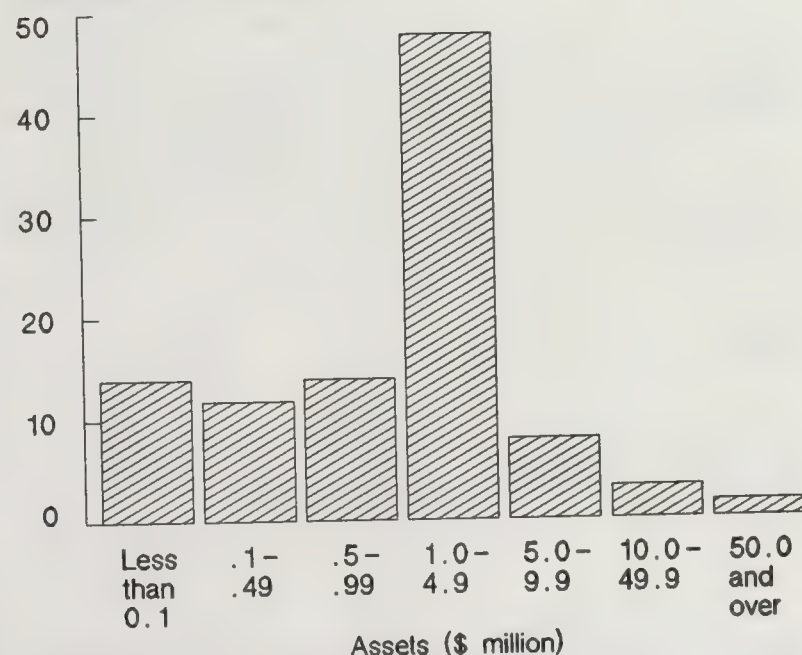


Memberships include duplication that cannot be eliminated using current reporting methods.

Chart 89

Distribution of farmer cooperatives by size of assets

% of farmer cooperatives



1987 data.

Farmer Cooperatives

Value of farm products marketed by farmer cooperatives increased 5.9 percent and supplies handled dropped 5.5 percent in 1987. The 24 cooperatives with gross business of \$500 million or more accounted for a greater percentage (38.3 percent) of total gross dollar volume than the 4,606 cooperatives with business of less than \$15 million (21.5 percent).

Chart 90

Distribution of farmer cooperative business by size of cooperative

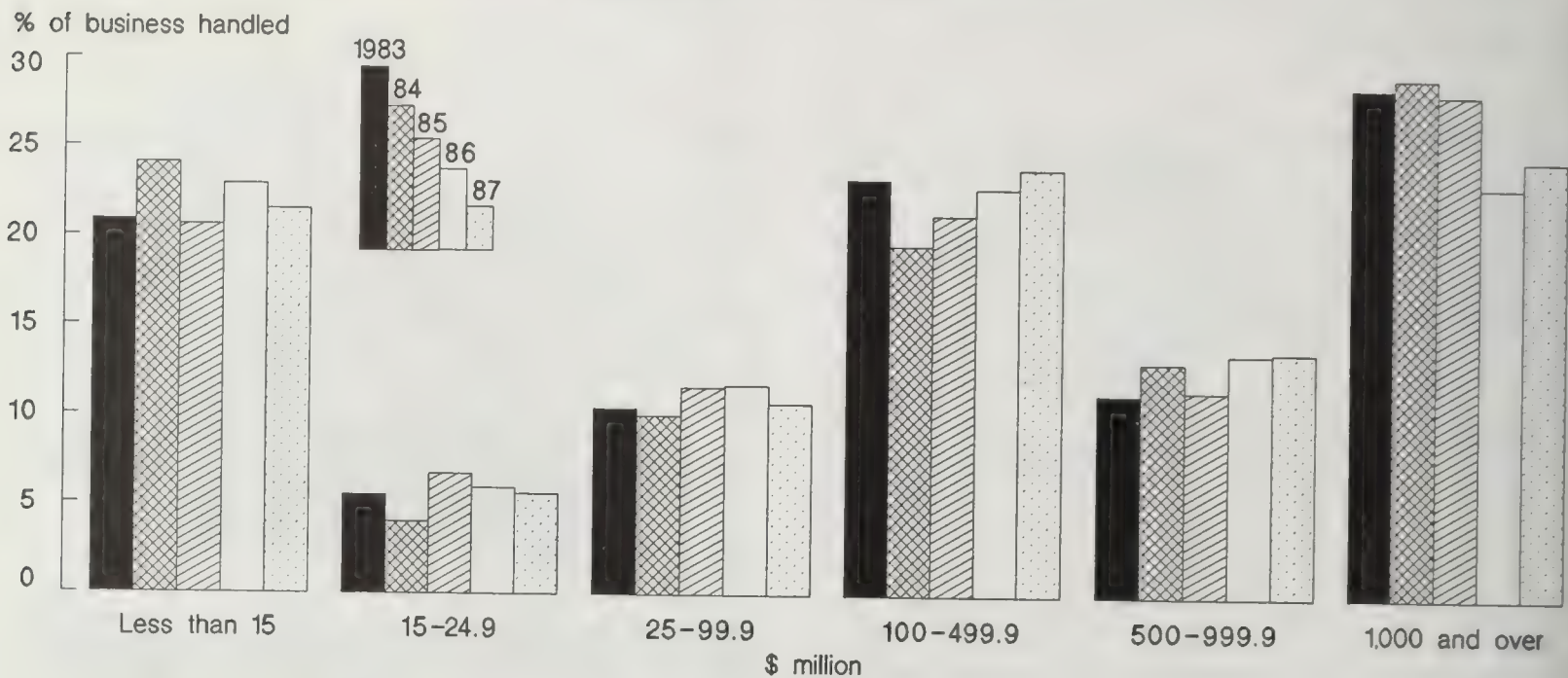
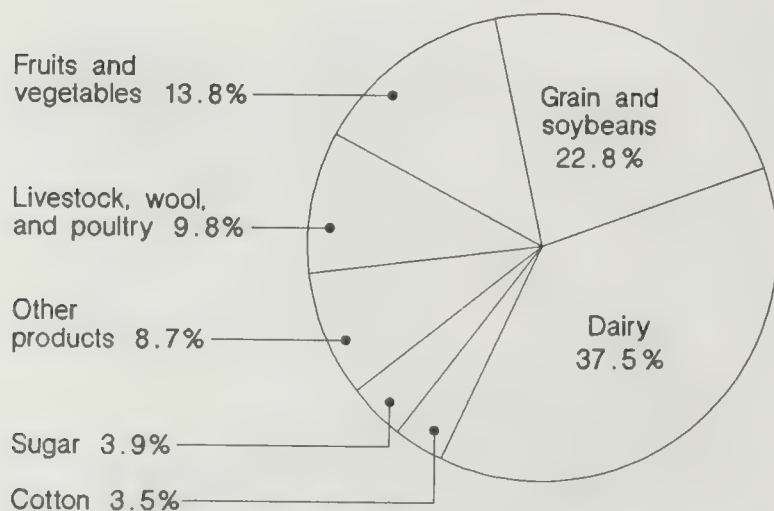


Chart 91

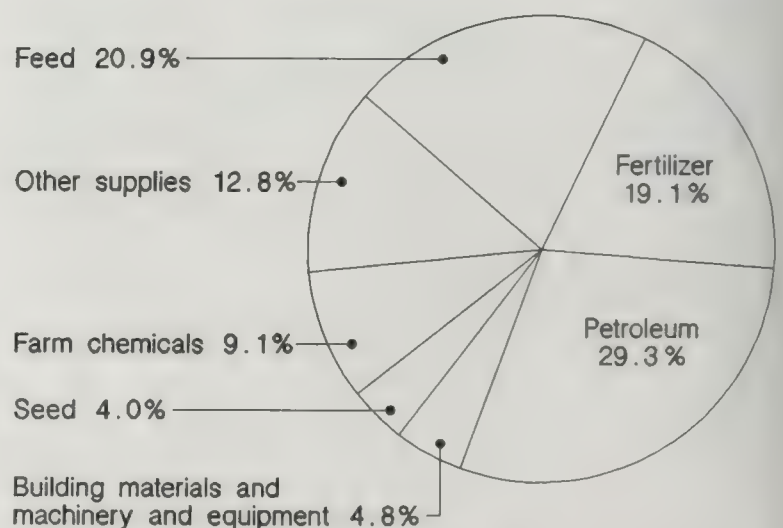
Farm products marketed by farmer cooperatives



1987 data. Total net marketing business = \$44.2 billion. Other products include dry edible beans and peas, nuts, rice, tobacco, and miscellaneous products.

Chart 92

Farm supplies handled by farmer cooperatives



1987 data. Total net farm supply business = \$14.3 billion. Other supplies include containers, meats and groceries, and miscellaneous farm supplies.

Population

Net outmigration from nonmetro counties became widespread in the mid-1980's. Poverty is consistently higher among nonmetro children, and is especially high in families where the mother is raising the children by herself.

Chart 93
Nonmetro counties with net outmigration, 1980-83

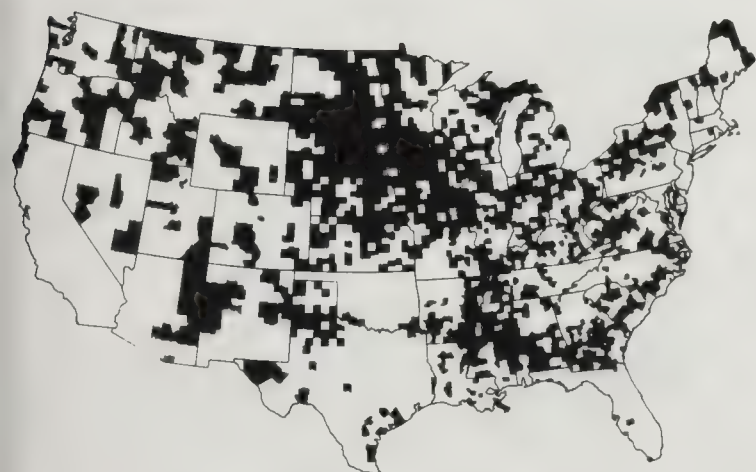


Chart 94
Nonmetro counties with net outmigration, 1983-88



Chart 95
Children under 18 years living with one parent

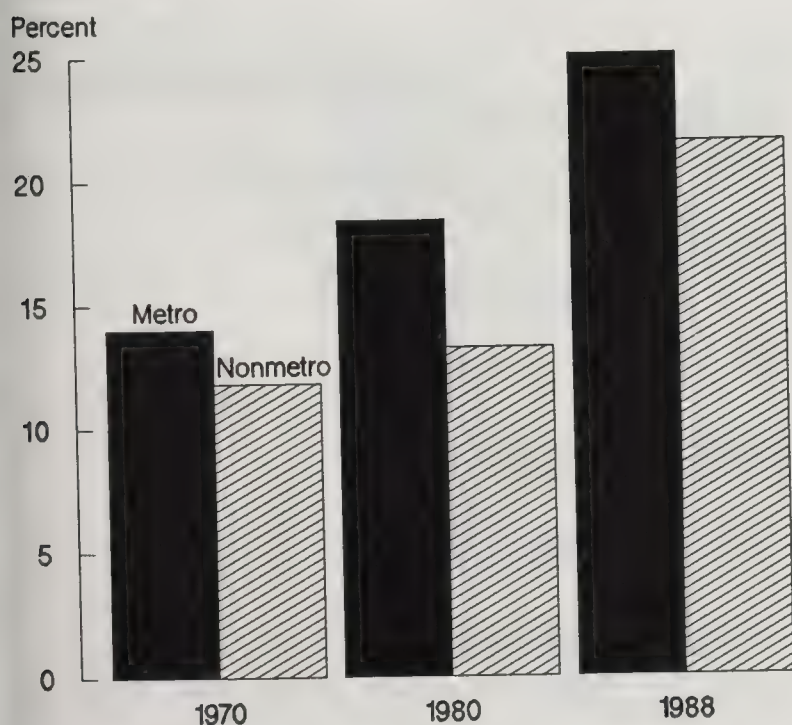
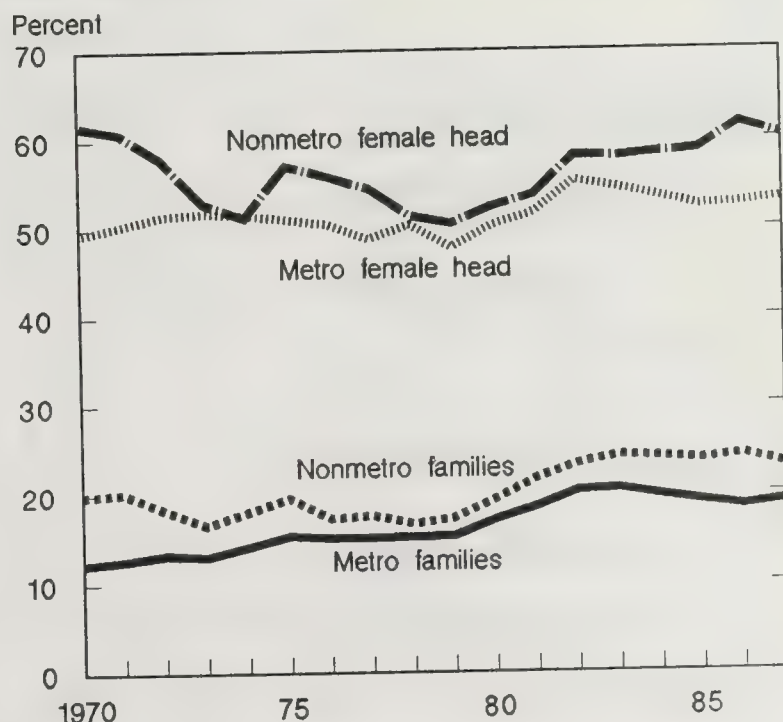


Chart 96
Children below poverty level, by family type and residence



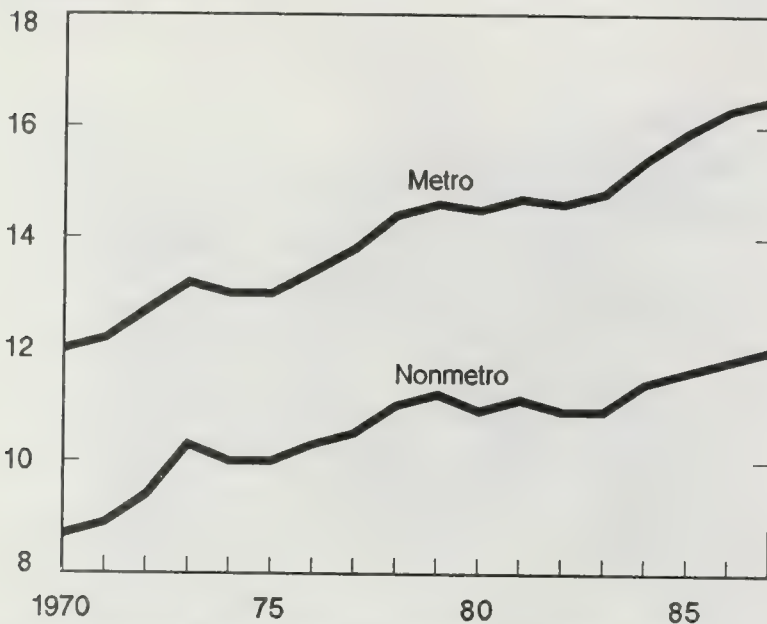
Personal Income

Metro residents consistently have higher income than nonmetro residents. Transfers grew faster than earnings during 1970-87. Social Security, medicare/medicaid, and other retirement/disability programs account for over 80 percent of government transfers to metro and nonmetro residents.

Chart 97

Trends in per capita income

Thousand 1987 \$

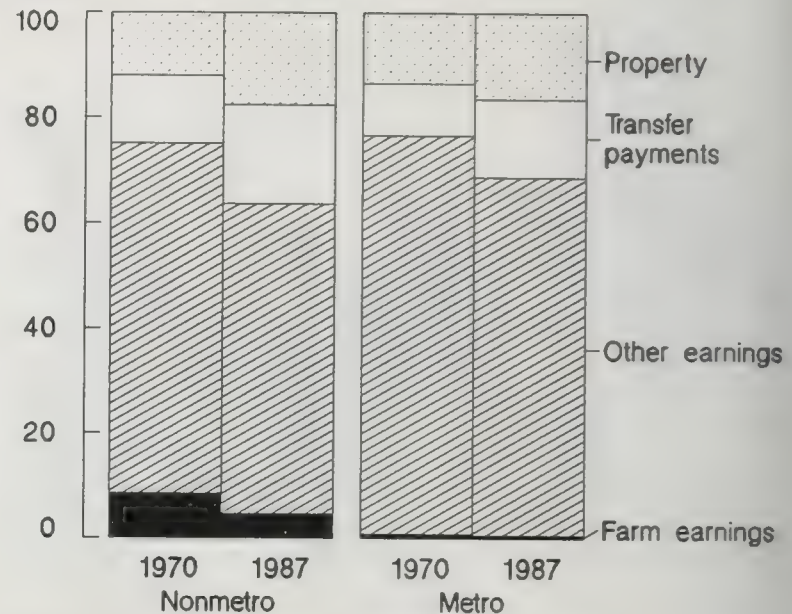


Source: Local Area Personal Income, U.S. Department of Commerce, Bureau of Economic Analysis.

Chart 98

Personal Income by source

Percent

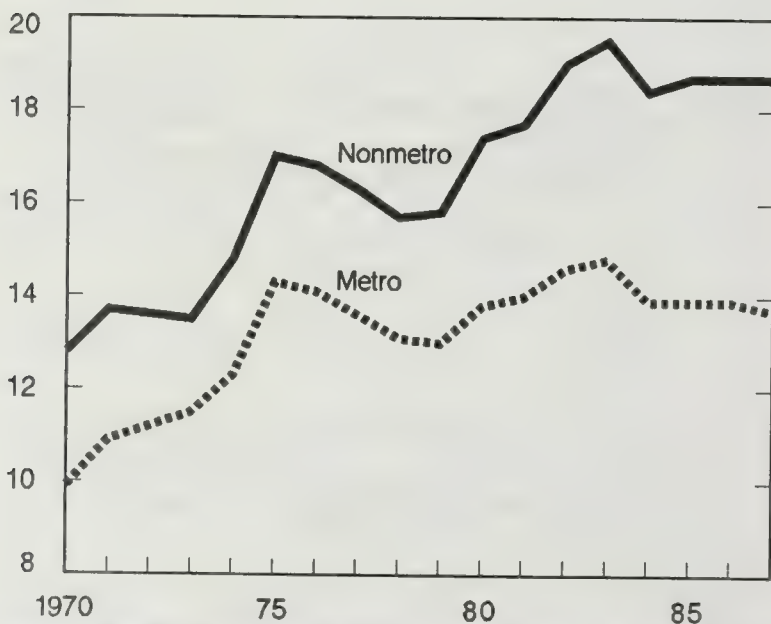


Source: Local Area Personal Income, U.S. Department of Commerce, Bureau of Economic Analysis.

Chart 99

Transfer payments as percentage of total personal income

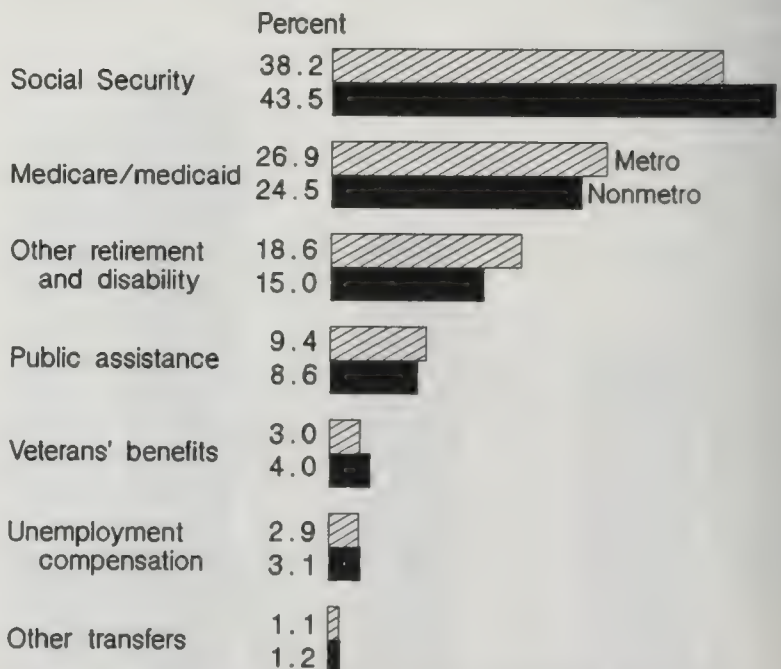
Percent



Source: Local Area Personal Income, U.S. Department of Commerce, Bureau of Economic Analysis.

Chart 100

Government transfer payments to individuals

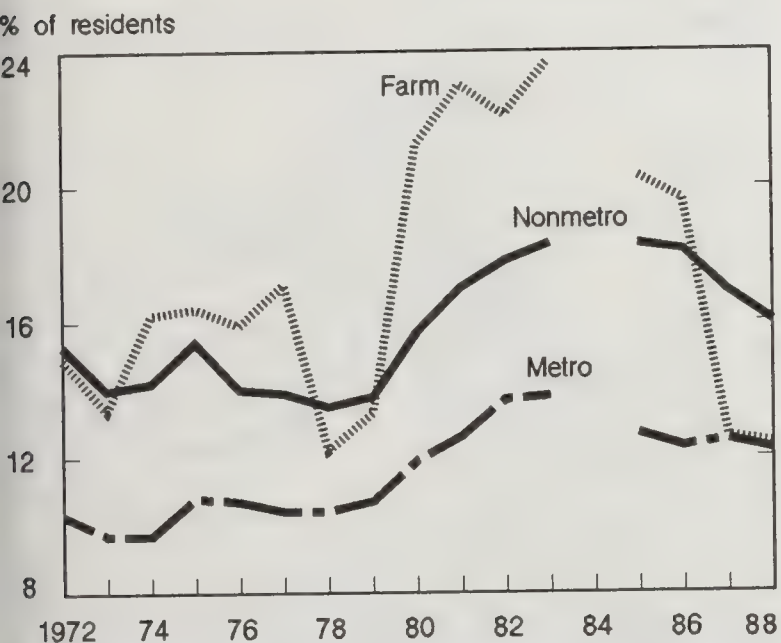


1987 data. Source: Local Area Personal Income, U.S. Department of Commerce, Bureau of Economic Analysis.

Poverty

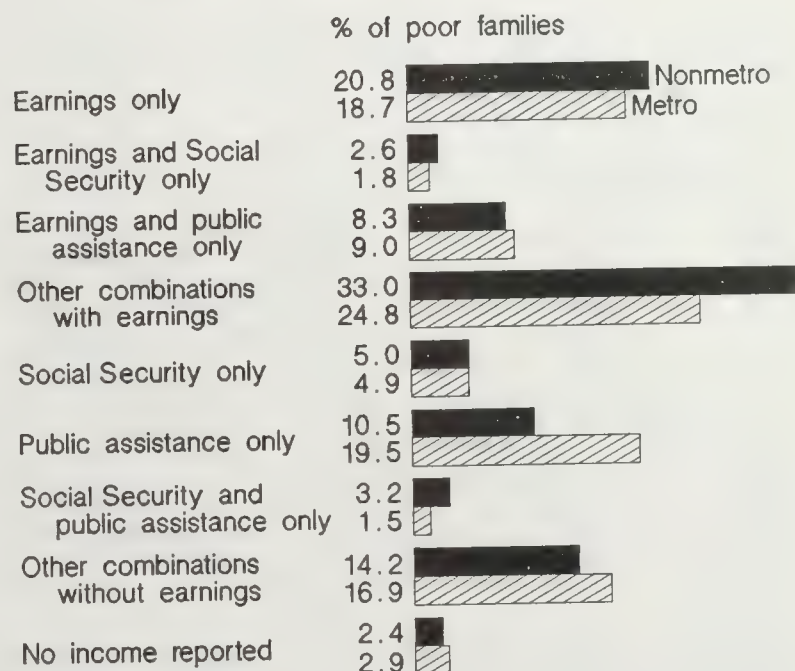
The poverty rate is higher in nonmetro than metro areas. Farm poverty was very high in the early 1980's, but has declined since then. Most poor families work for at least part of their income. Elderly blacks and young black children living in nonmetro areas have very high poverty rates.

Chart 101
Poverty rates



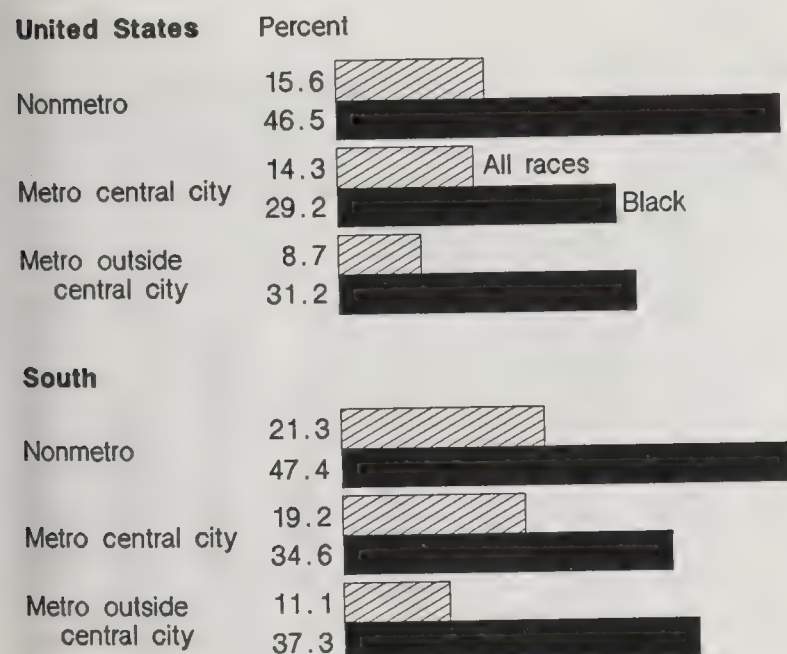
The farm poverty rate is the proportion of all residents living on farms who are poor. Data for 1984 not available. Source: Current Population Survey, Bureau of the Census.

Chart 102
Poor families by sources of income



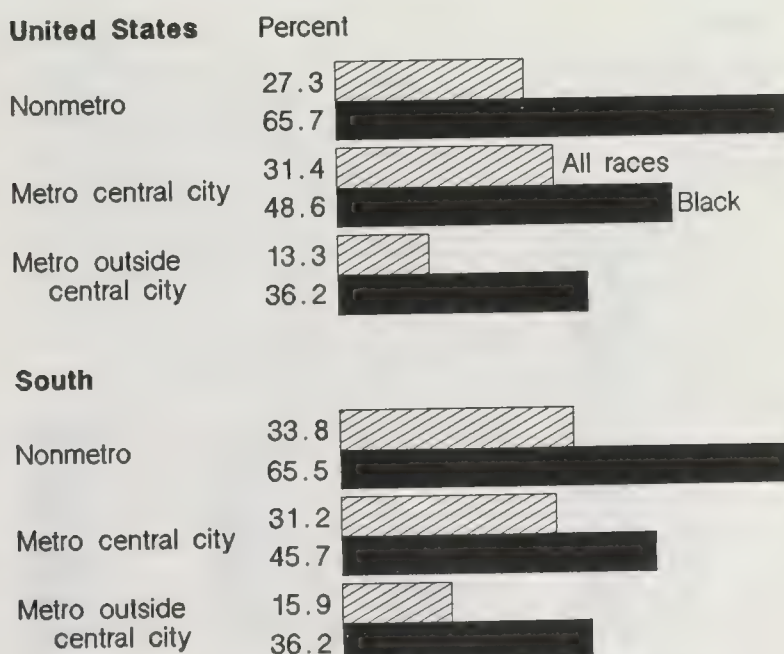
1987 data. Source: Current Population Survey, Bureau of the Census.

Chart 103
Percentage of the elderly in poverty



1987 data. The elderly are persons 65 and over. Source: Current Population Survey, Bureau of the Census.

Chart 104
Percentage of young children in poverty



1987 data. Young children are under 6 and live in families. Source: Current Population Survey, Bureau of the Census.

Employment

Nonmetro economies outside the Northeast had lower employment growth and higher unemployment than metro areas between 1982 and 1988.

Chart 105

Employment change from previous year

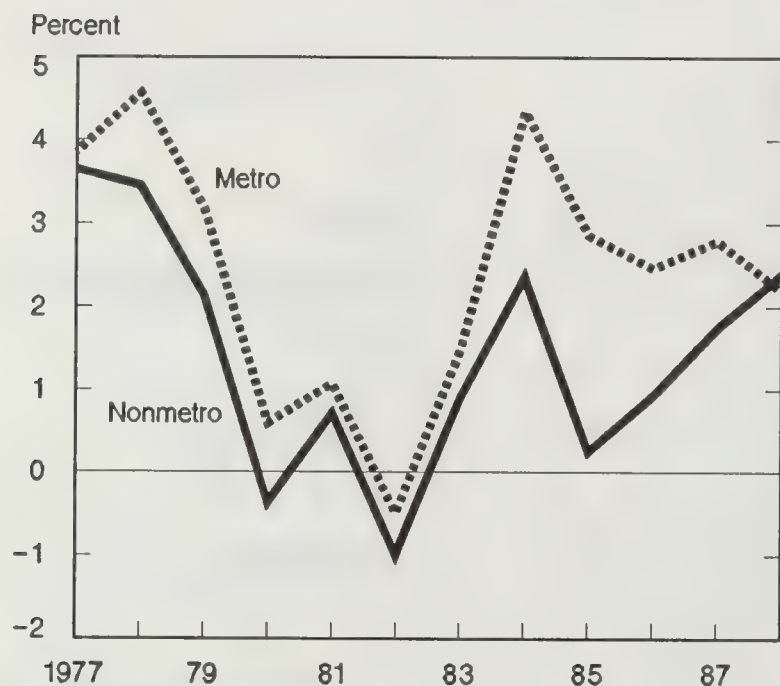


Chart 106

Unemployment rates for metro and nonmetro areas

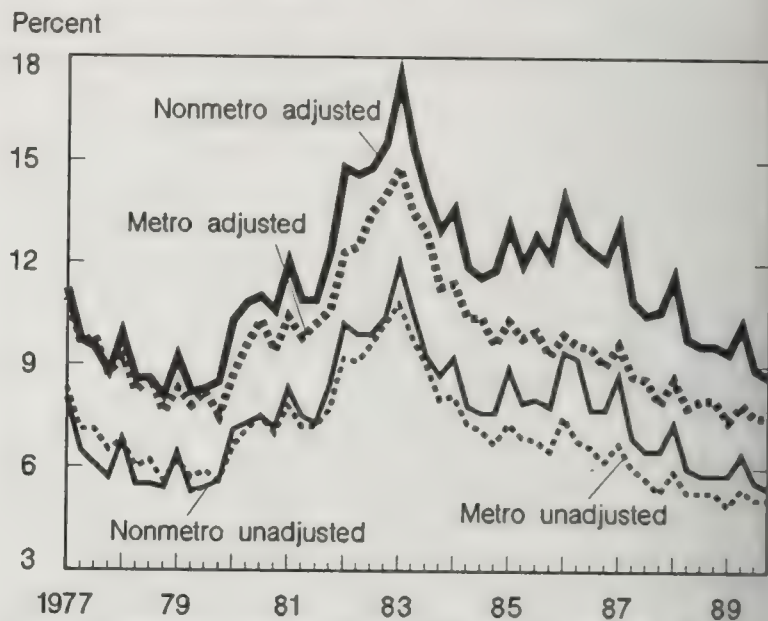


Chart 107

Employment growth by region, 1982-88

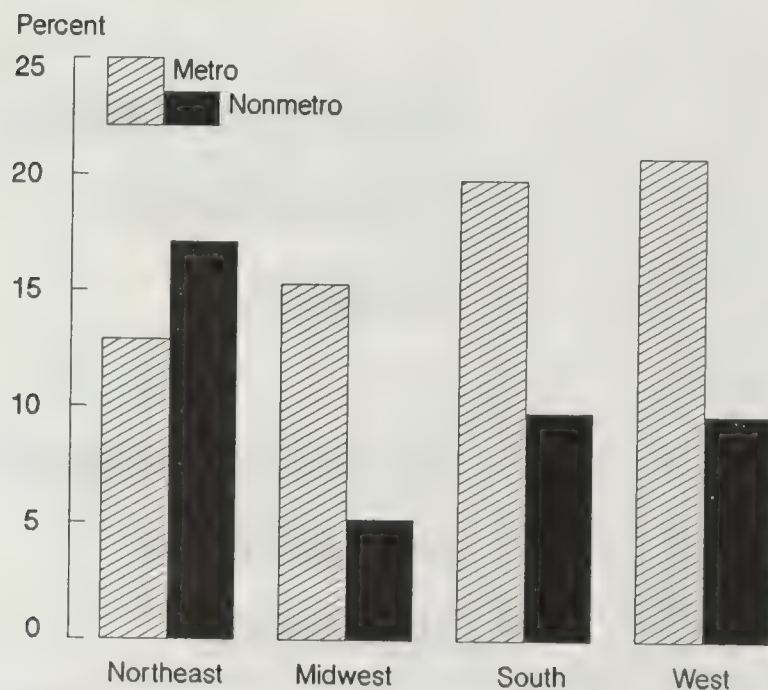
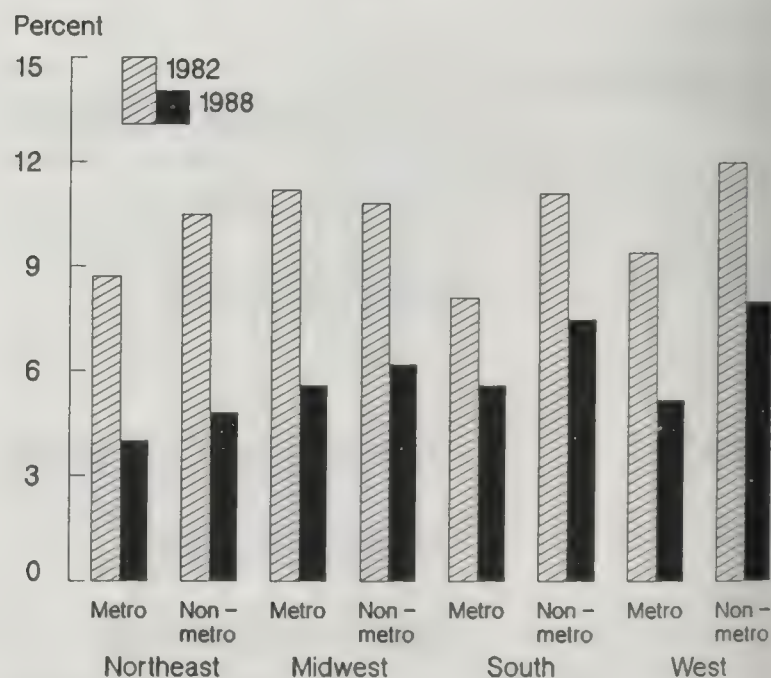


Chart 108

Unemployment by region



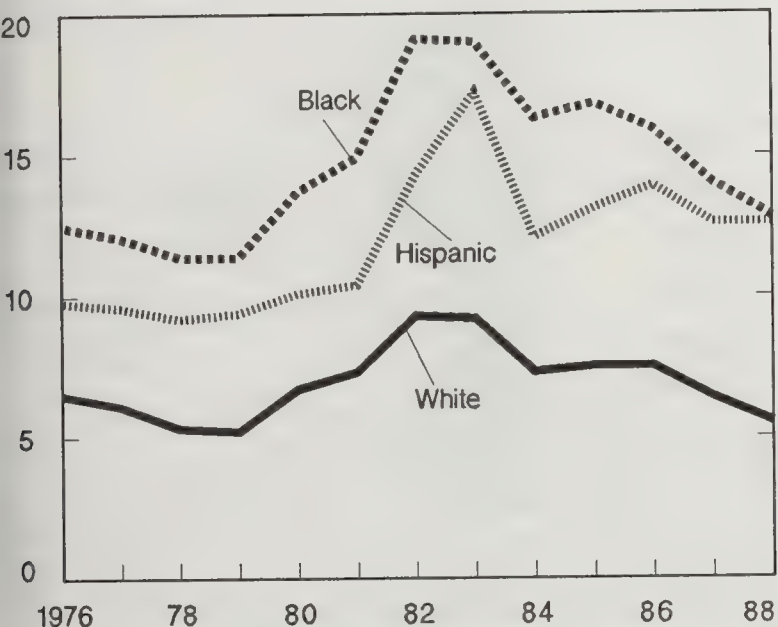
Employment

Employment grew at a faster rate in nonmetro areas than metro areas in 1988, for the first time since the mid-1970's. However, teenagers and minorities continue to experience relatively high levels of unemployment. Nonmetro employment growth rates were above 15.4 percent in 13 States between 1982 and 1988, while the nonmetro unemployment rate was over 1.5 times the U.S. average in 11 States.

Chart 109

Nonmetro unemployment by race/ethnicity

Percent



Beginning third quarter 1985, CPS nonmetro definition based on 1980 Census.
Source: Current Population Survey.

Chart 110

Nonmetro unemployment by age

Percent

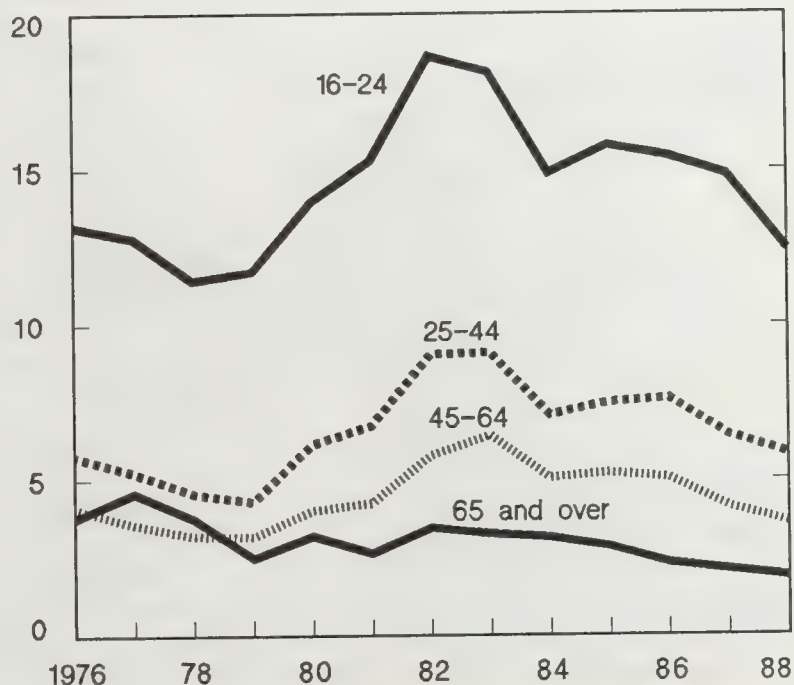
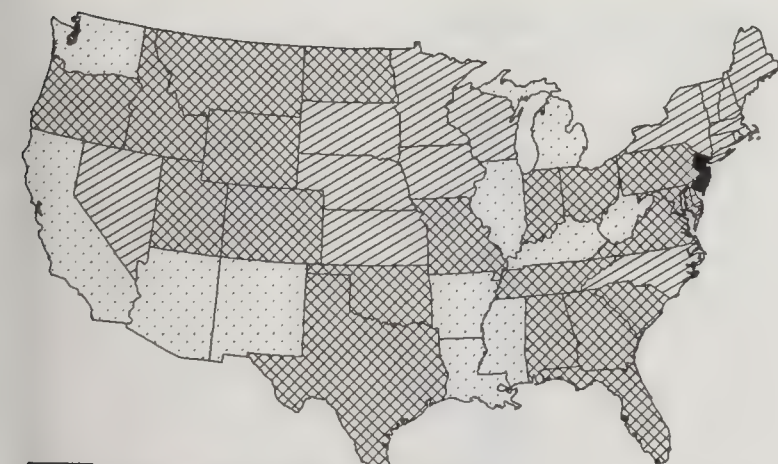


Chart 111

Nonmetro unemployment by State, 1988

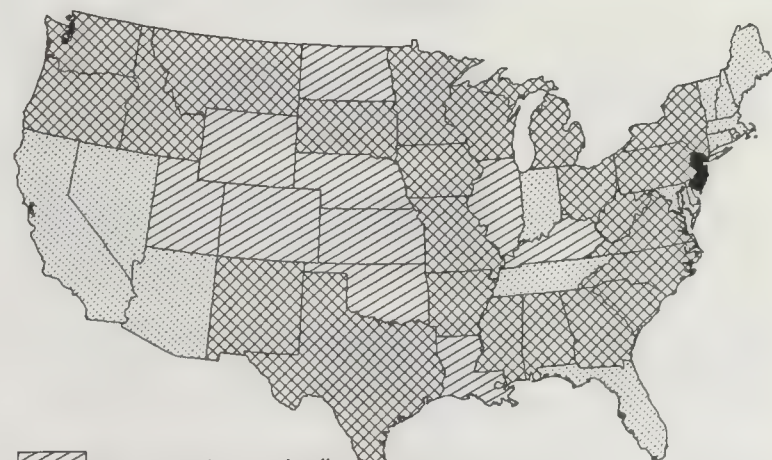


U.S. average (5.5%) or less
1-1.5 times U.S. average
Over 1.5 times U.S. average
No nonmetro counties

Source: Bureau of Labor Statistics.

Chart 112

Nonmetro employment growth by State, 1982-88



No growth or decline
Up to U.S. average (15.4%)
Above the U.S. average
No nonmetro counties

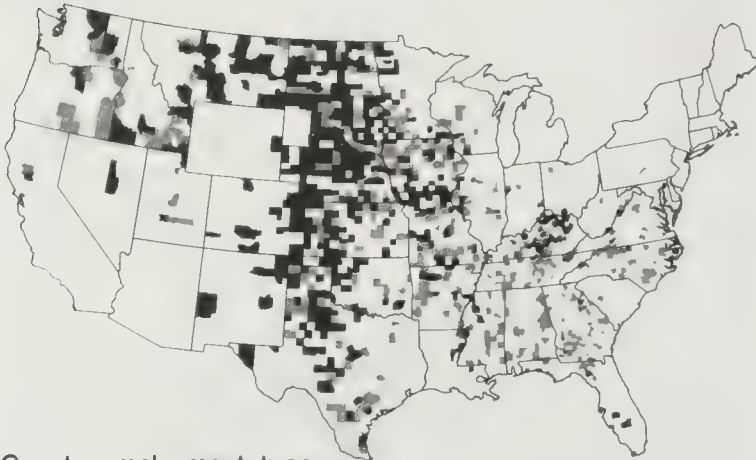
Source: Bureau of Labor Statistics.

Food and Fiber System Employment

The food and fiber system is a major employer in nonmetro America. In 800 counties (785 non-metro and 15 metro) farming and farm-related industries employ a third or more of the local labor force. In 1986, the system accounted for nearly 30 percent, or 5.9 million, of the jobs in nonmetro America.

Chart 113

Agribusiness counties, 1986

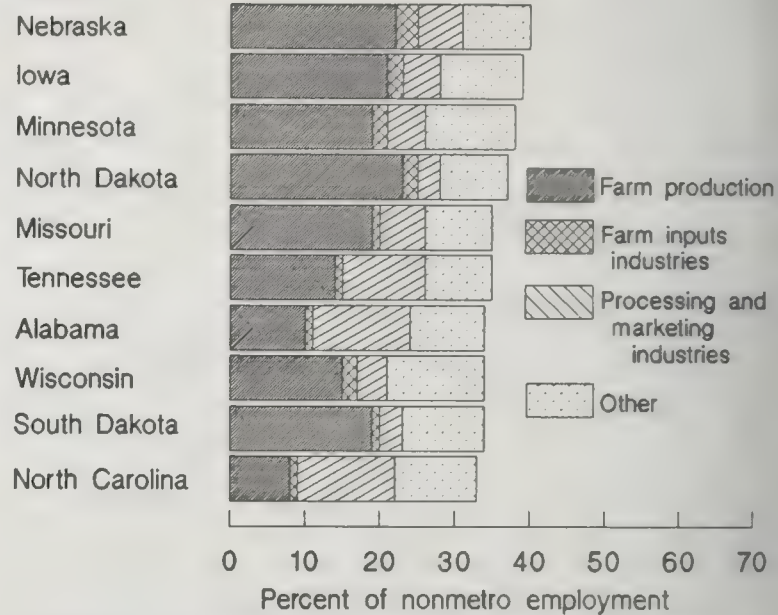


County employment type:

- Specialized (a third or more in farm production);
- Diversified (a third or more in farm production, agricultural input, and agricultural processing and marketing industries)

Chart 114

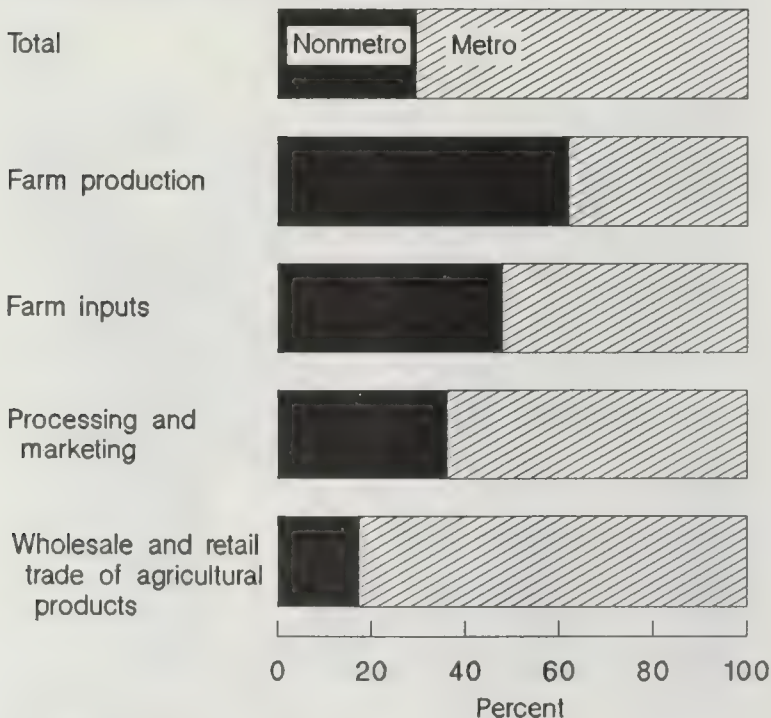
States with nonmetro areas most dependent on food and fiber sector employment



1986 data. Other category includes wholesale and retail trade of agricultural products.

Chart 115

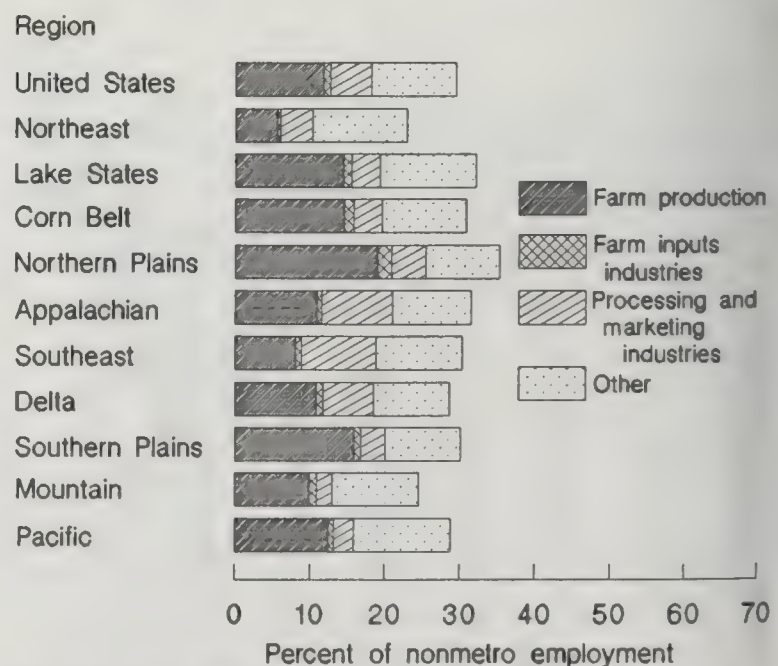
Location of food and fiber employment



1986 data.

Chart 116

Food and fiber employment in nonmetro areas

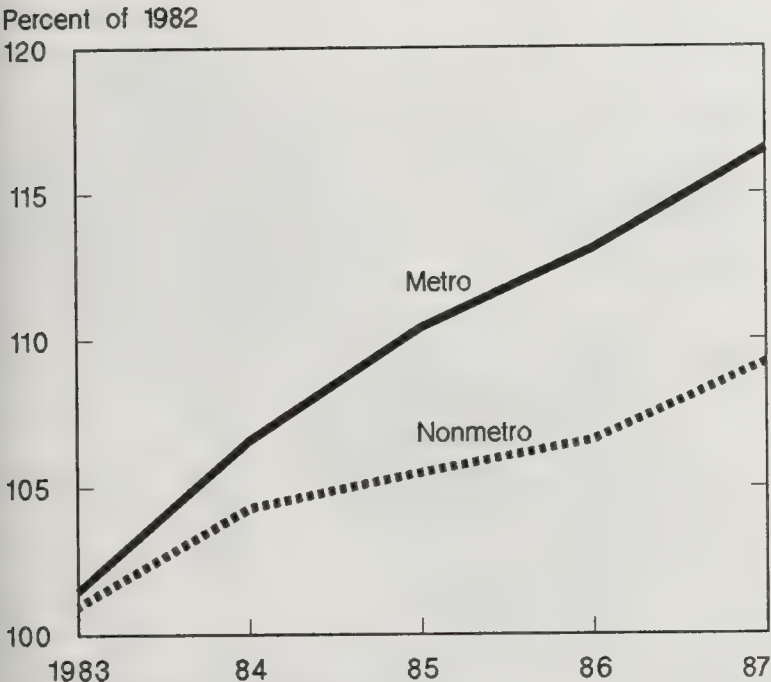


1986 data. Other category includes wholesale and retail trade of agricultural products.

Nonmetro Versus Metro Employment

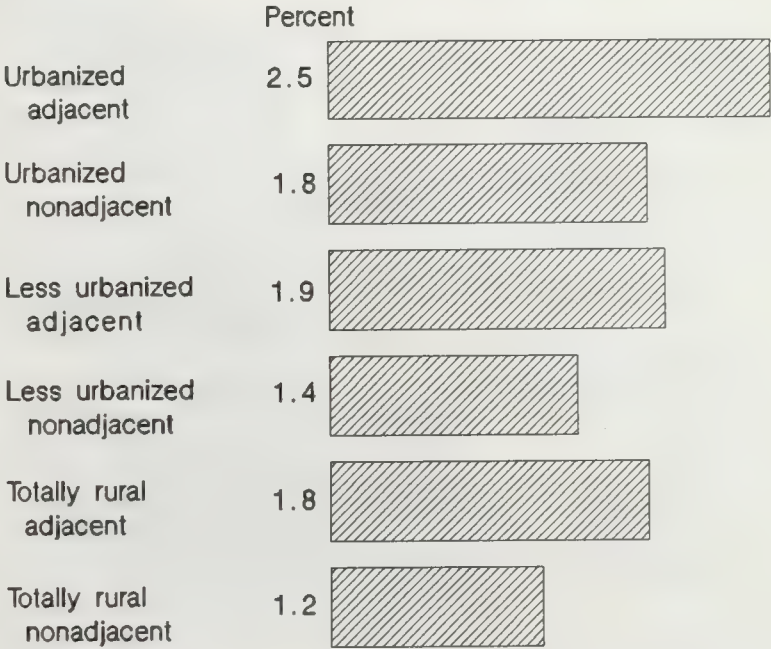
Nonmetro counties adjacent to metro areas had better growth than more remote counties. Nonmetro employment was stable or increased in all States except Louisiana, North Dakota, Oklahoma, Wyoming, Nebraska, and West Virginia.

Chart 117
Metro and nonmetro employment change since 1982



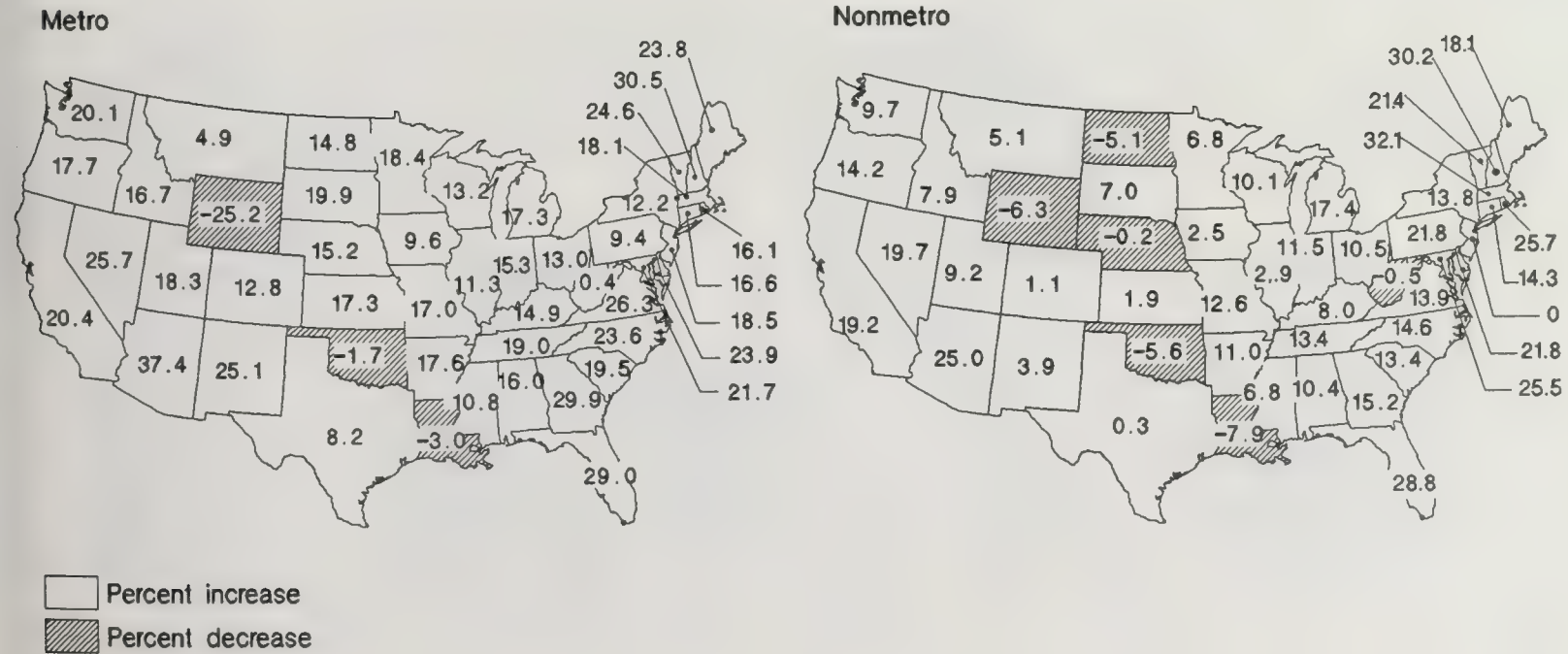
Source: Bureau of Economic Analysis.

Chart 118
Average annual growth rates for nonmetro counties, 1982-87



Source: Bureau of Economic Analysis

Chart 119
Metro and nonmetro employment change by State, 1982-87



Industry Employment

Employment in all industries grew more in metro than in nonmetro areas except for the natural resources and manufacturing industries. Regionally, the West has the smallest percentage of manufacturing jobs. The agricultural sector is largest in the Midwest.

Chart 120

Average annual employment change by industry, 1982-87

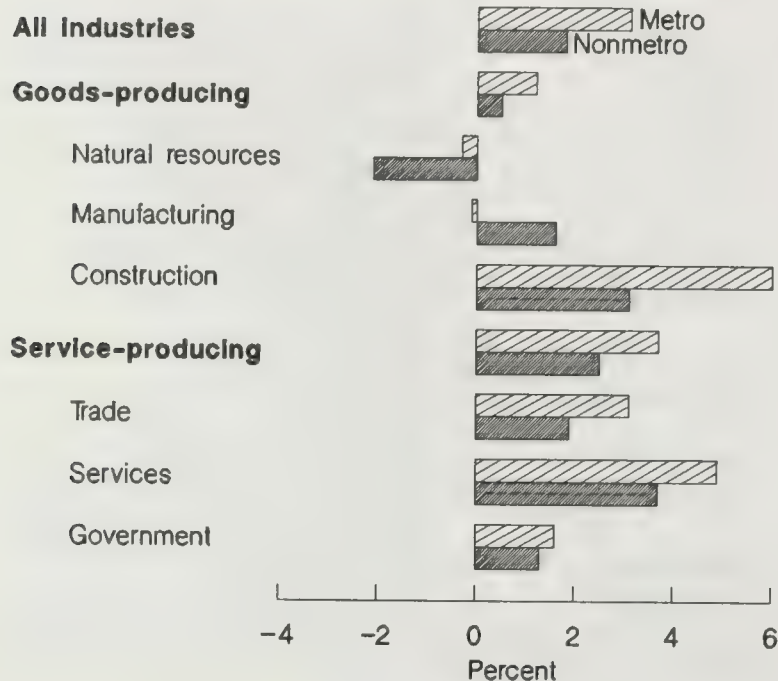
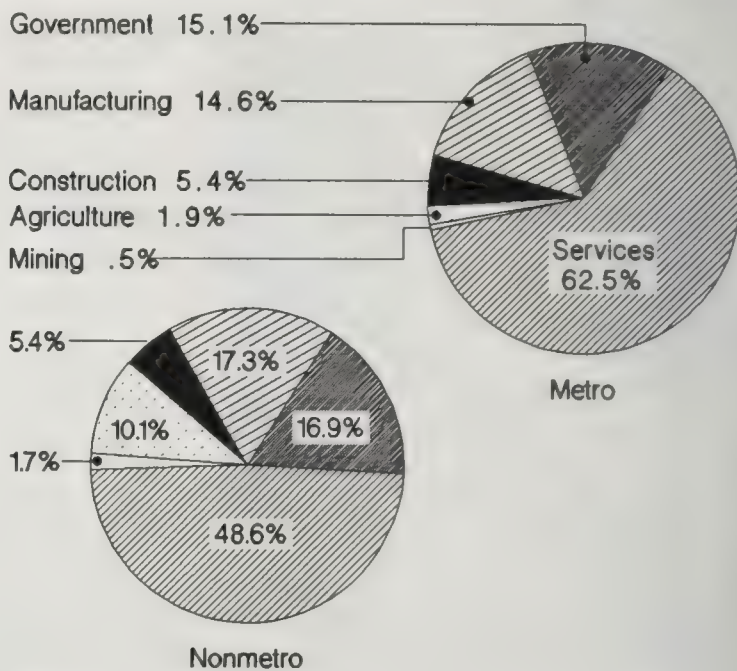


Chart 121

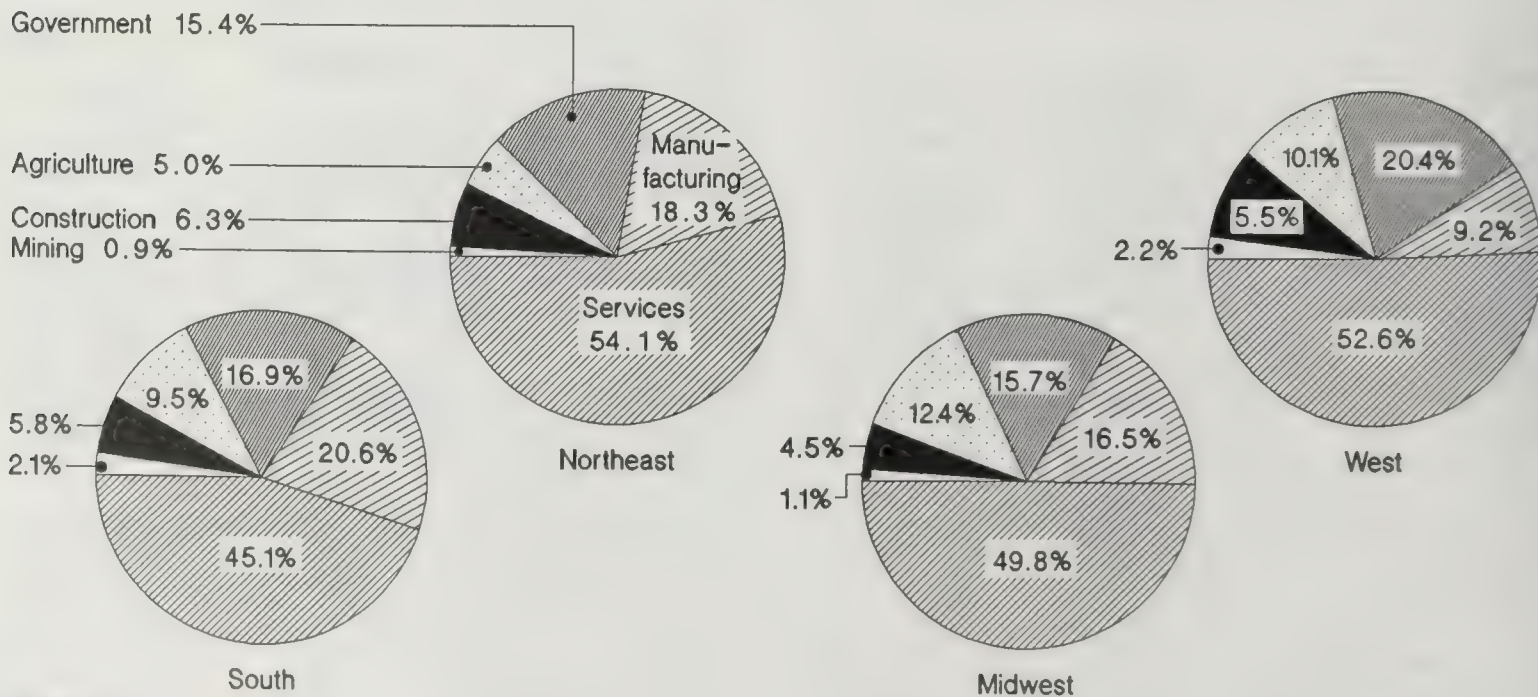
Importance of industries in metro and nonmetro areas



1987 data.

Chart 122

Regional importance of nonmetro industries

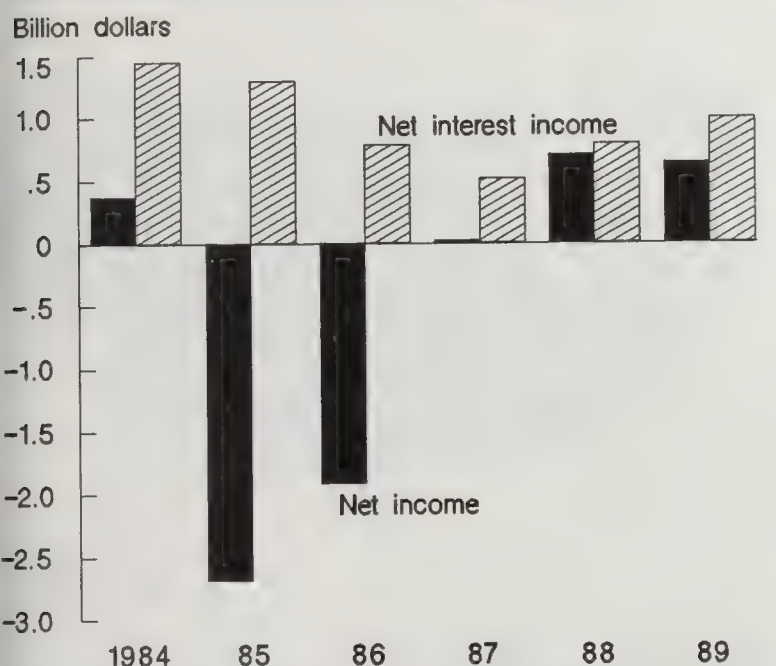


1987 data.

Farm Credit

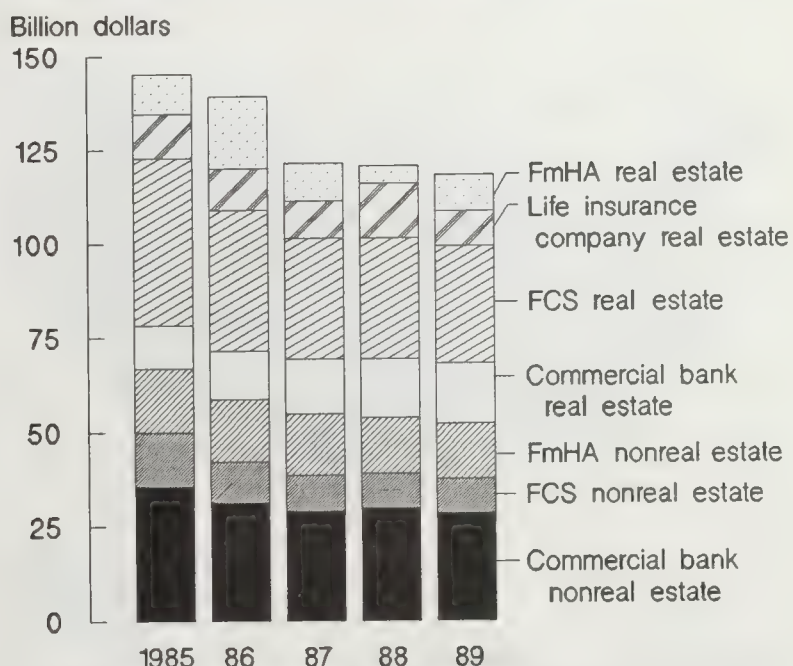
Provision for loan losses caused the Farm Credit System's net income to be at its lowest in 1985-86. Overall farm debt has declined since then, and the distribution of debt has changed slightly. Agricultural interest rates remained strong in 1989 and continued to be highly differentiated between lenders.

Chart 123
**Comparison of the farm credit system:
Net interest income and net income**



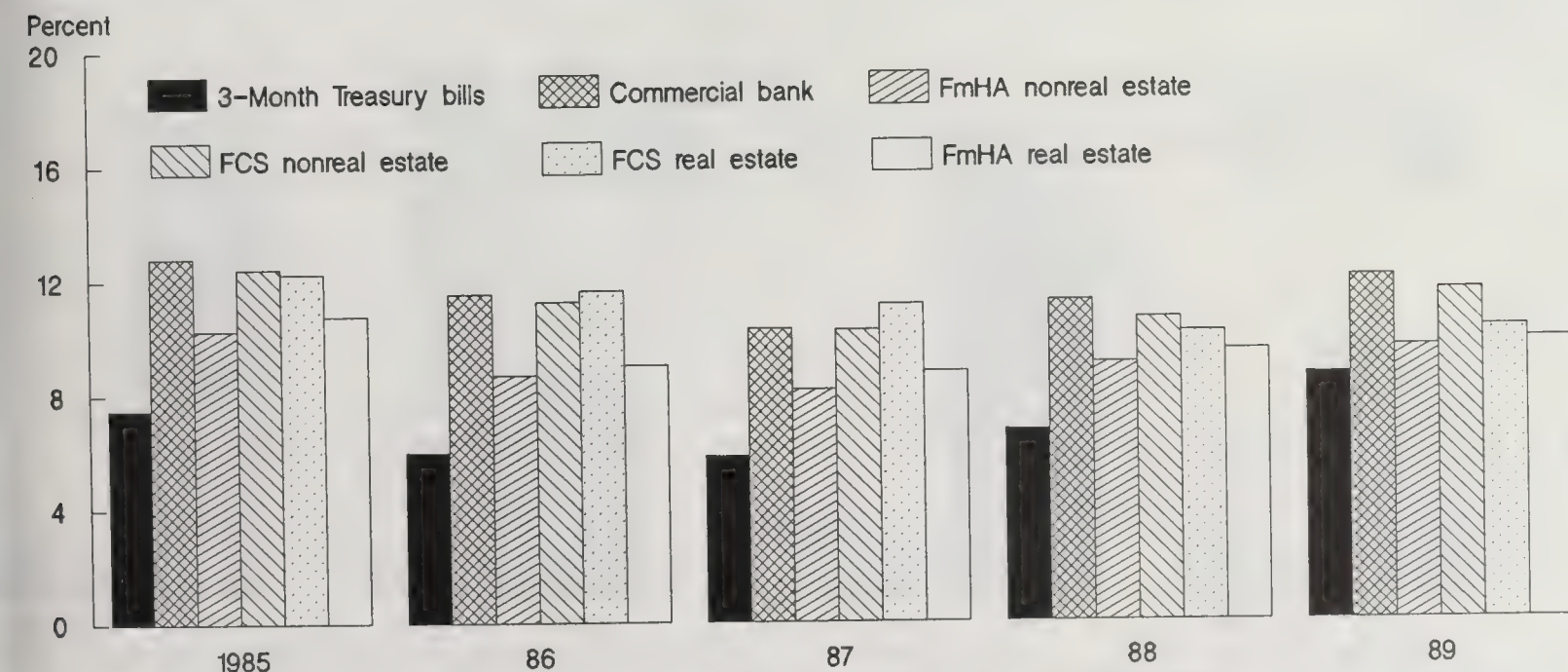
Net interest income minus provisions for loan losses and other charges, equals net income. Values for 1989 are annualized, second quarter data.

Chart 124
Loans outstanding by major agricultural lenders



End of year data except for 1989. Includes real estate and nonreal estate loans. Source: Agricultural Finance Data book, 1989.

Chart 125
Selected agricultural interest rates



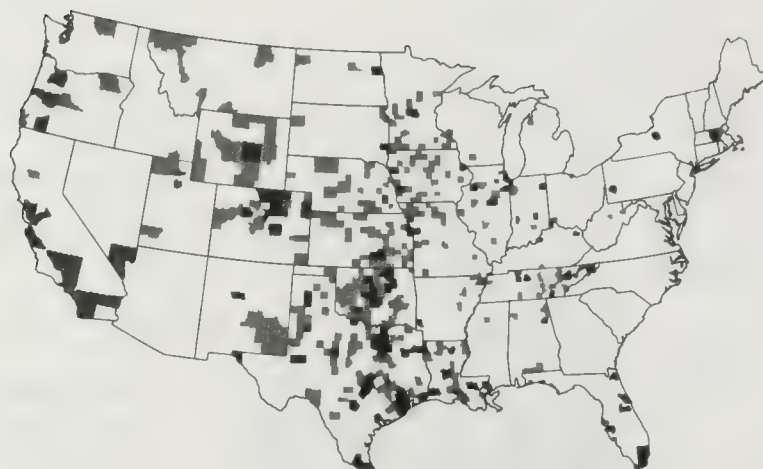
Yearly data except for 1989. Source: USDA AFO-32, selected banks of the FCS, and Agricultural Finance Data Book, various issues.

Banking

Commercial banks headquartered in rural areas constituted 48 percent of all failures from 1983 to 1988, but only 33 percent of failures in 1988. Commercial banks headquartered in rural areas outnumber urban-based banks, but hold only 12 percent of all bank deposits. About 31 percent of the savings and loans (S&L's) are headquartered in rural areas, but hold only about 9 percent of S&L assets.

Chart 126

Commercial bank failures by county, 1983-88



■ Metro ■ Nonmetro

Chart 127

Savings and loan failures by county, 1983-88



■ Metro ■ Nonmetro

Chart 128

Nonmetro/metro banks and bank assets by size

% of U.S. total

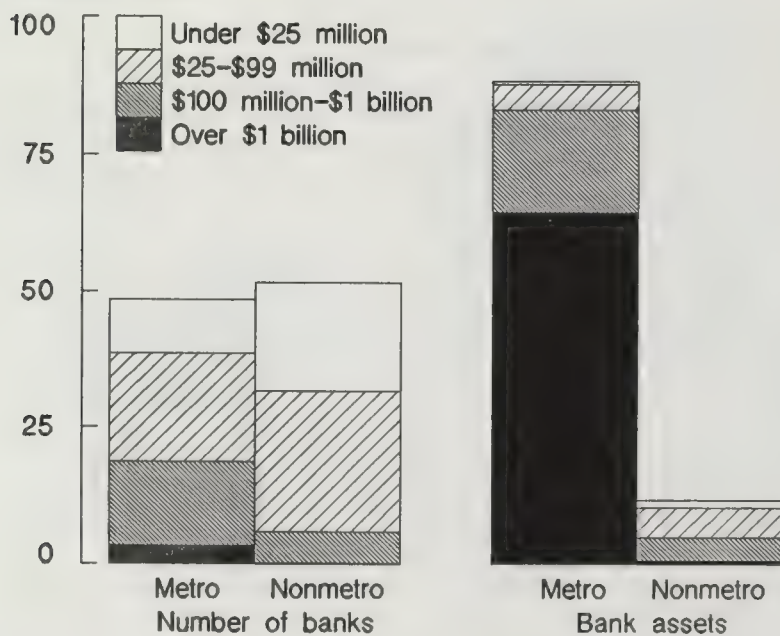
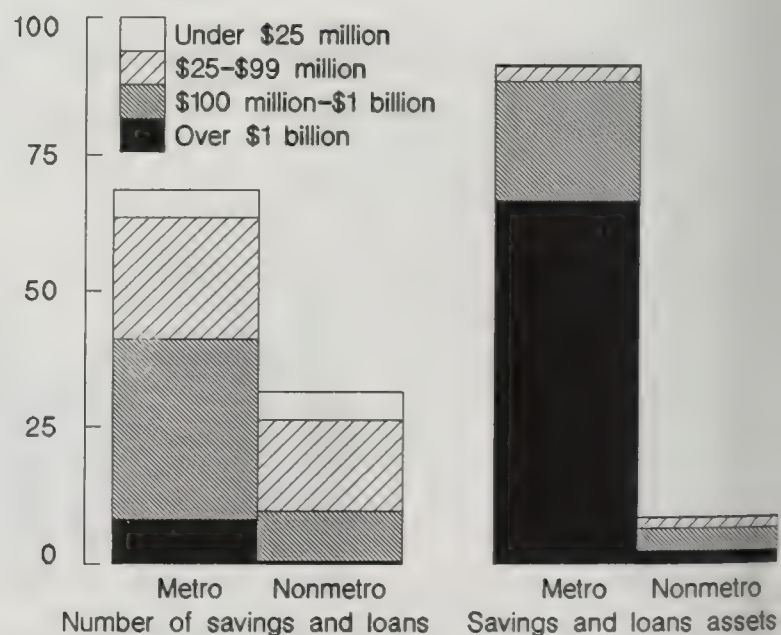


Chart 129

Nonmetro/metro savings and loans assets by size

% of U.S. total



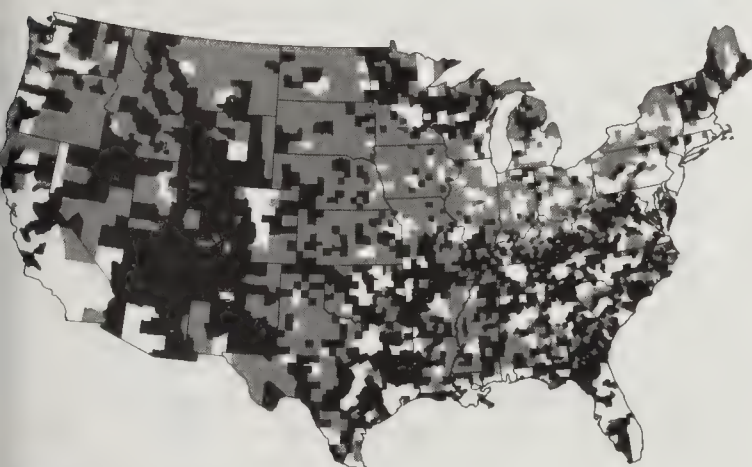
December 31, 1988 data. U.S. commercial banks.

December 31, 1988 data.

Earnings

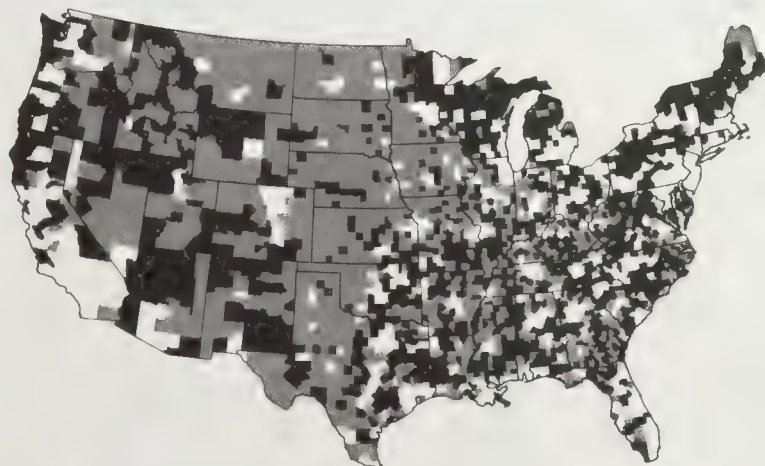
Total earnings grew at an annual rate of 2 percent for the nonmetropolitan United States during the 1969-86 period. This growth is due to growth in employment rather than any change in earnings per job. Growth was strongest in the South and West, but year-to-year stability of earnings growth was highest in the Northeast.

Chart 130
Earnings growth in nonmetropolitan counties, 1969-86



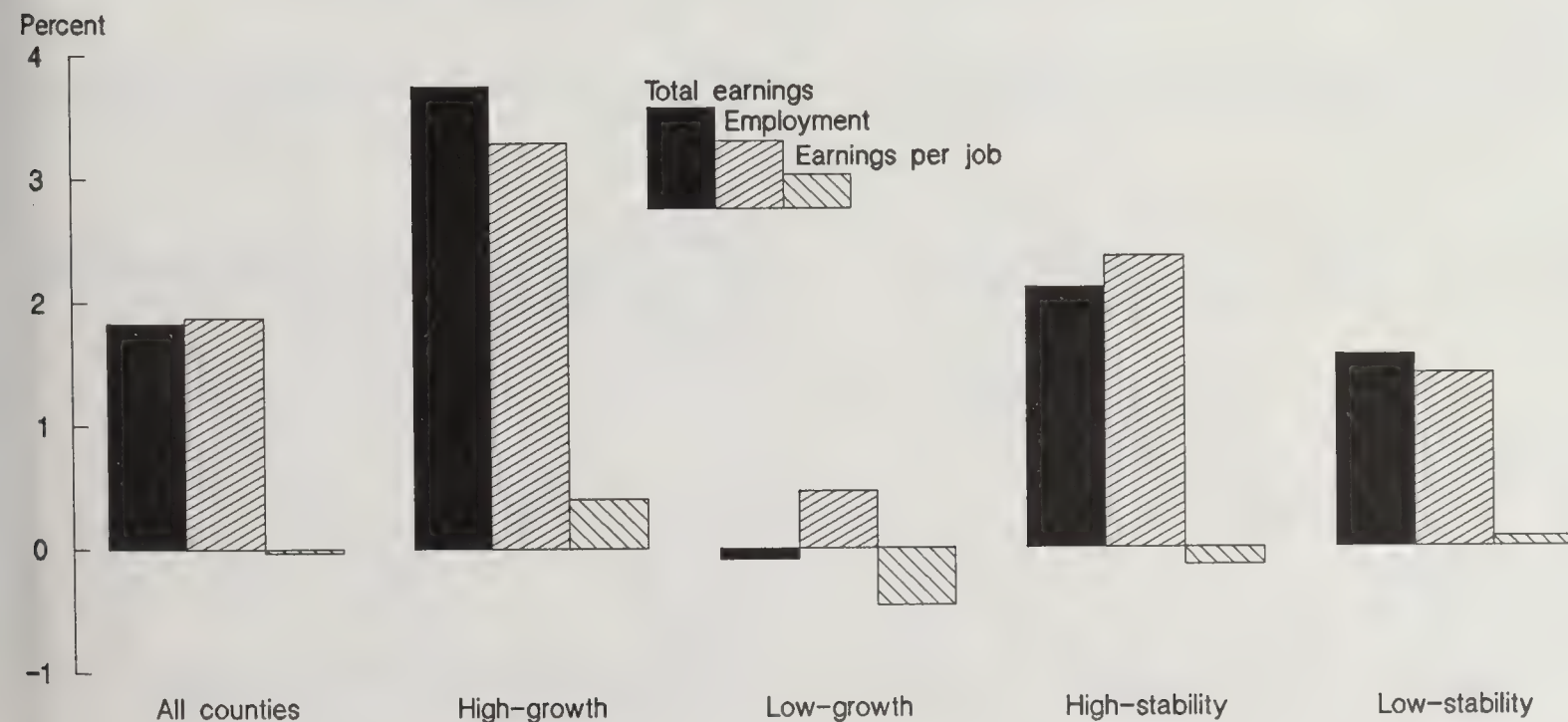
High-growth
Low-growth
Metro

Chart 131
Stability of earnings growth in nonmetropolitan counties, 1969-86



High-stability
Low-stability
Metro

Chart 132
Components of earnings growth in nonmetropolitan counties, 1969-86



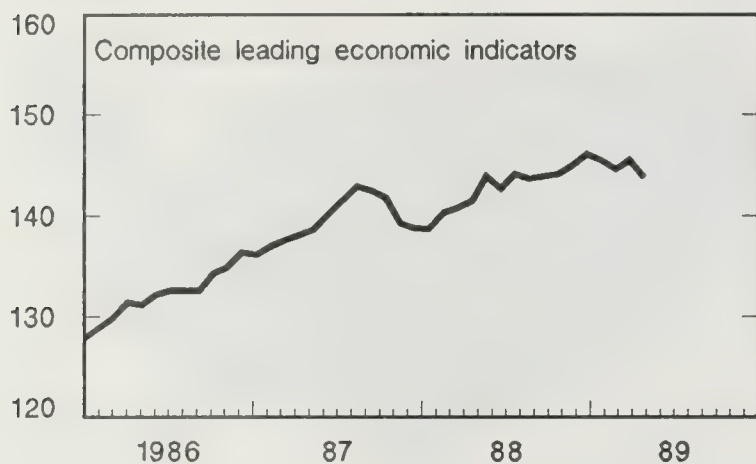
Economic Indicators

A sluggish manufacturing sector slowed growth in real gross national product in 1989.

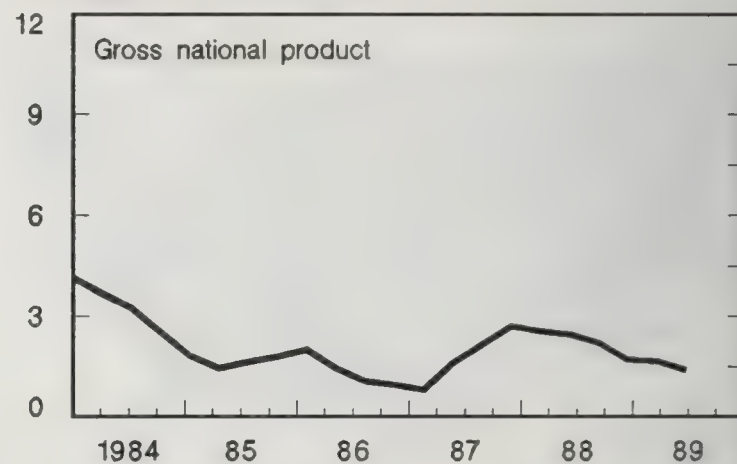
Chart 133

General economic indicators: Industry

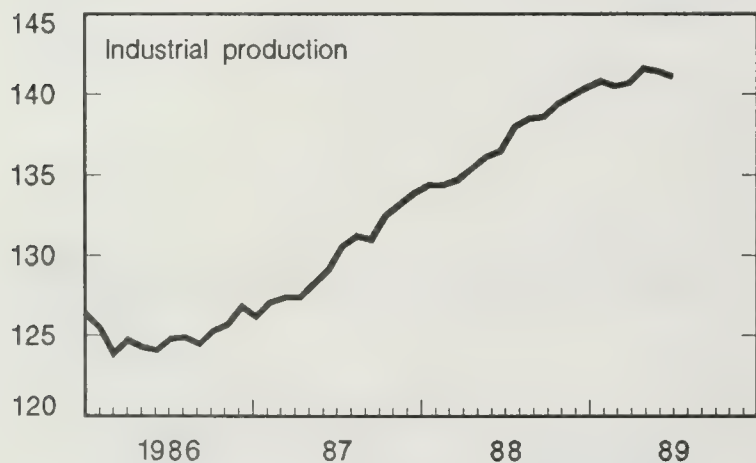
% of 1982



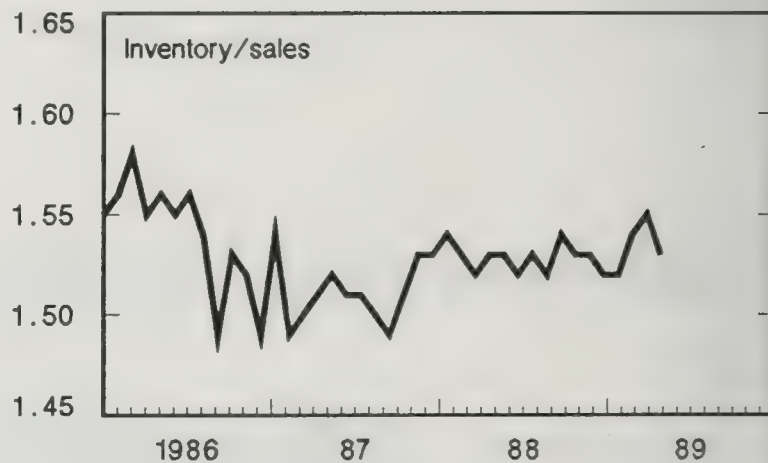
% change from previous year



% of 1977



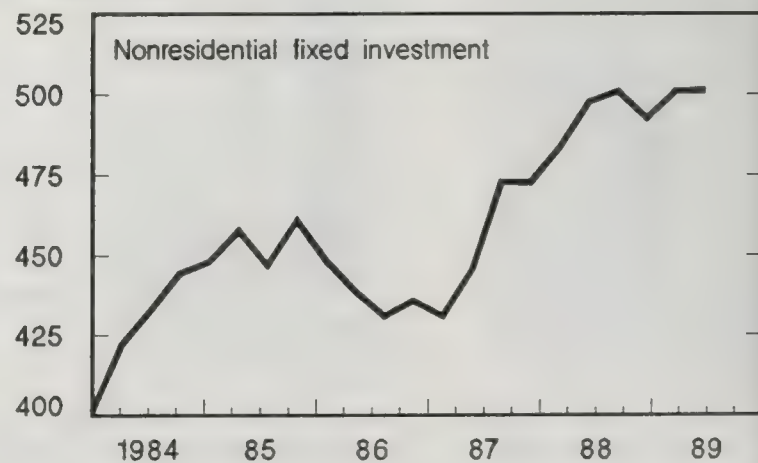
Ratio



\$ billion



\$ billion 1982



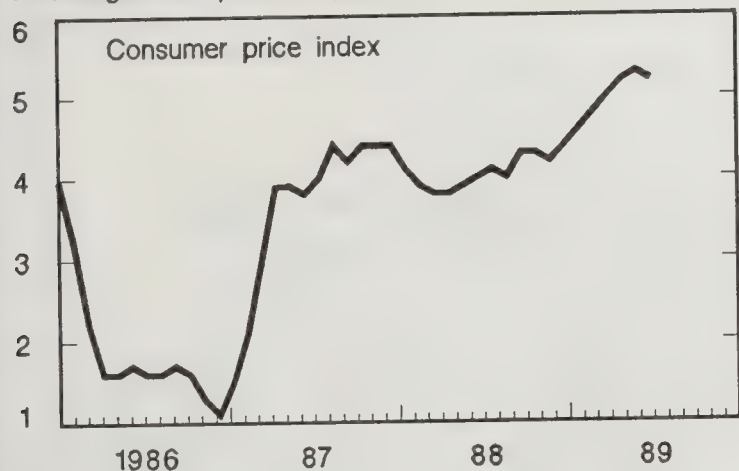
Economic Indicators

Inflation increased and interest rates rose, but the unemployment rate remained at decade lows and real consumer income continued to climb in 1989.

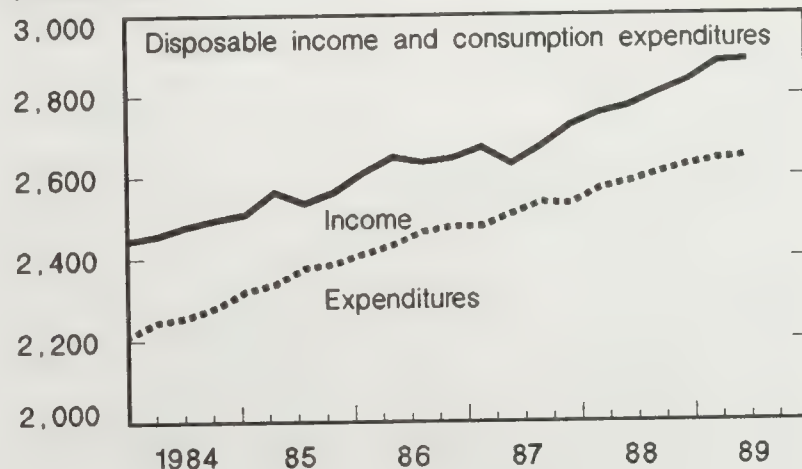
Chart 134

General economic indicators: Personal economy

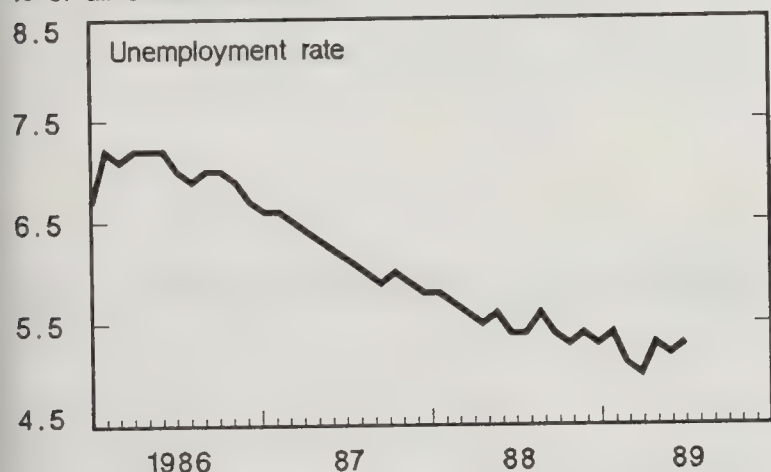
% change from previous year



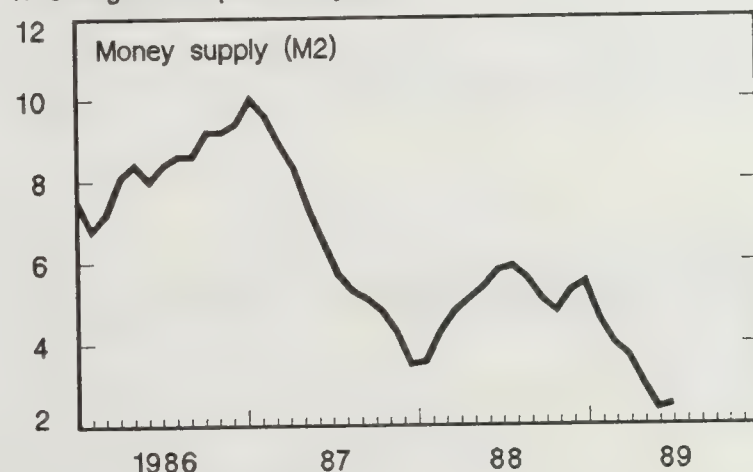
\$ billion 1982



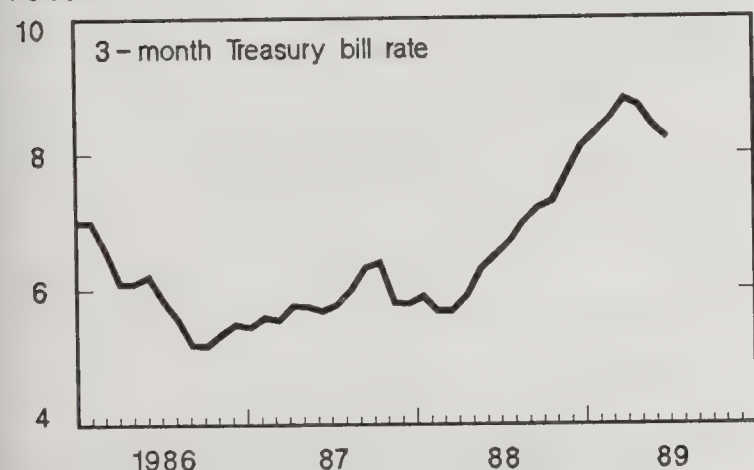
% of all civilian workers



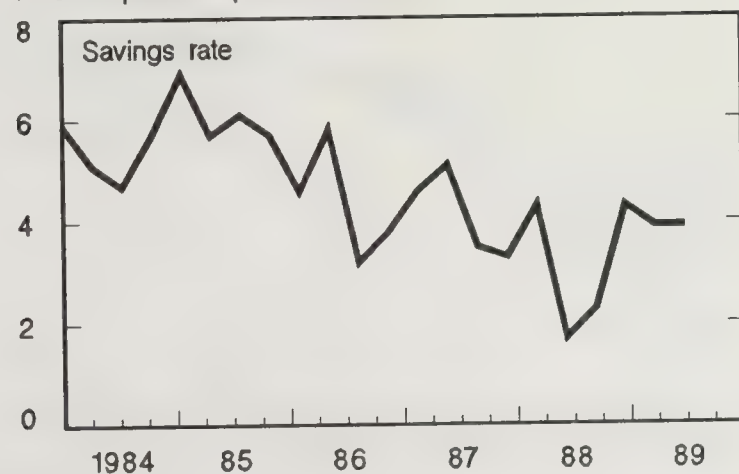
% change from previous year



Percent



% of disposable personal income



Consumer Prices

Retail food prices rose nearly 6 percent in 1989, the greatest increase since 1981. The rise was the result of lower supplies of some products due to lingering effects from the drought of 1988 and poor weather conditions in the first half of 1989. Strong consumer demand for meats also played a role in higher prices.

Chart 135

Consumer price index for food

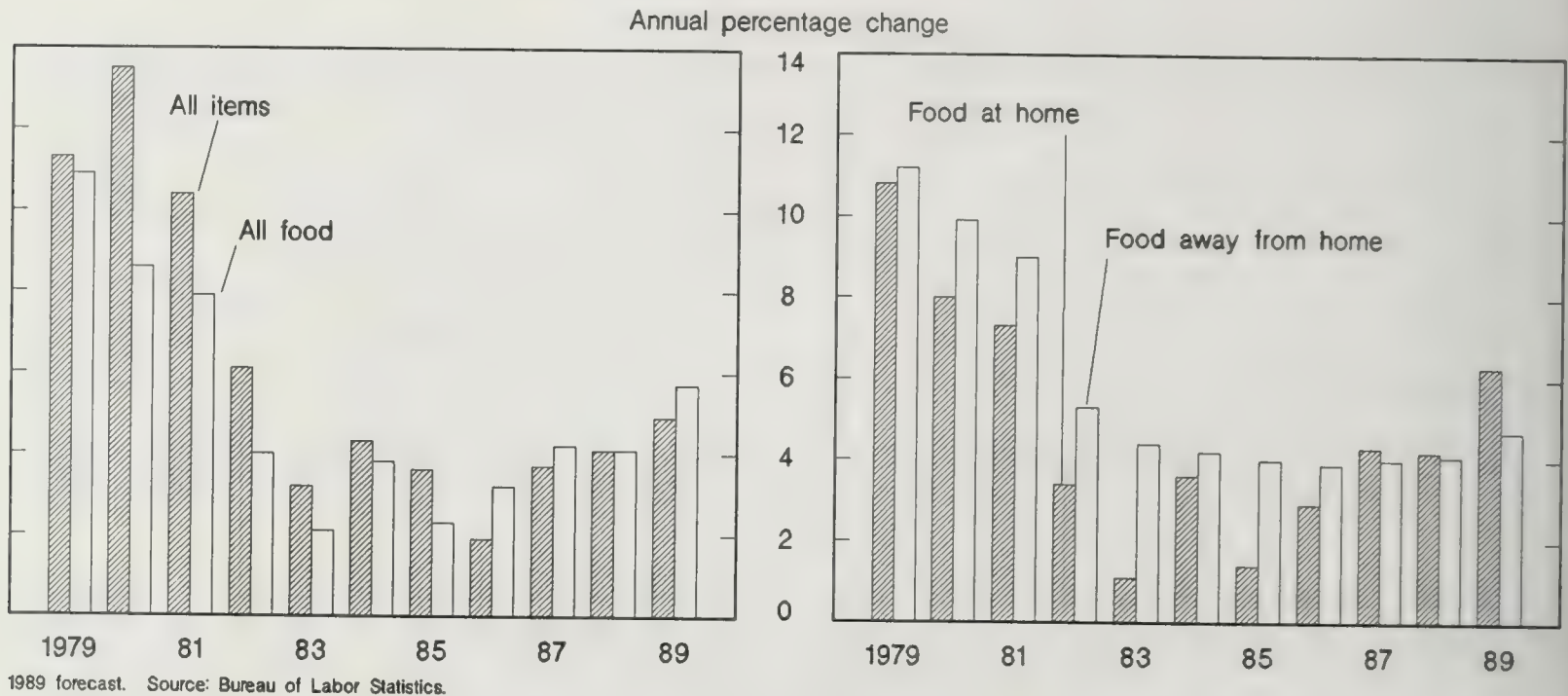
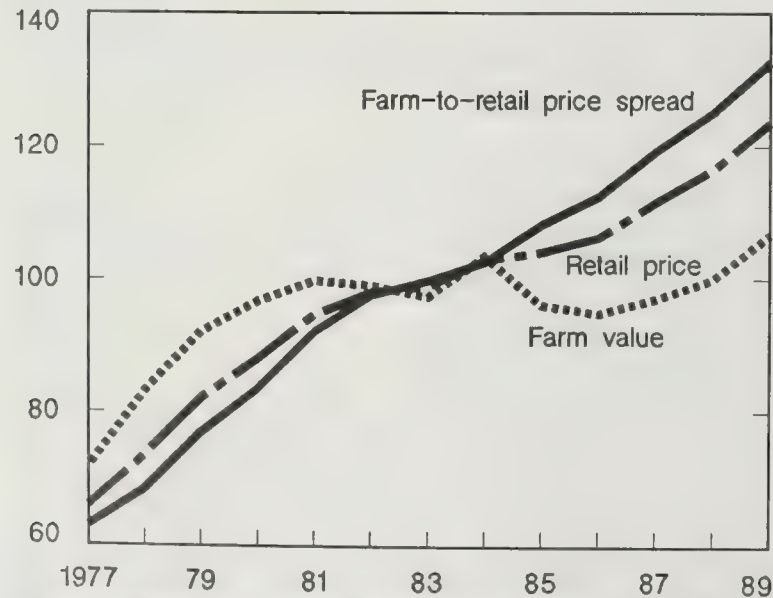


Chart 136

Retail price, farm value, and price spread for food

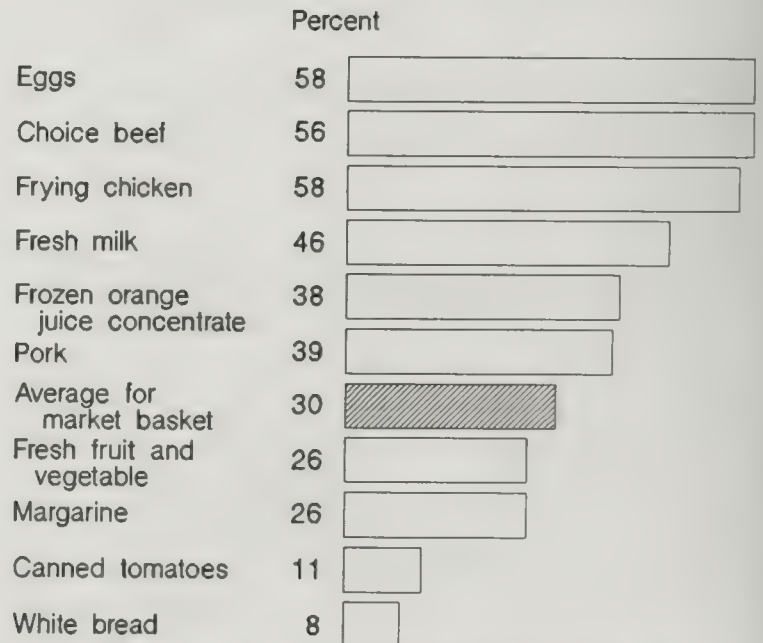
% of 1982-84



Data for a market basket of foods sold in retail stores. Retail price is that paid by consumers. Farm value is prices received by farmers for commodities. Price spread represents all charges for processing and distribution.

Chart 137

Farm value share of retail food prices



1988 data. Farm value share is the proportion the farmer receives from the dollar the consumer spends. The remainder of the dollar goes to marketing firms.

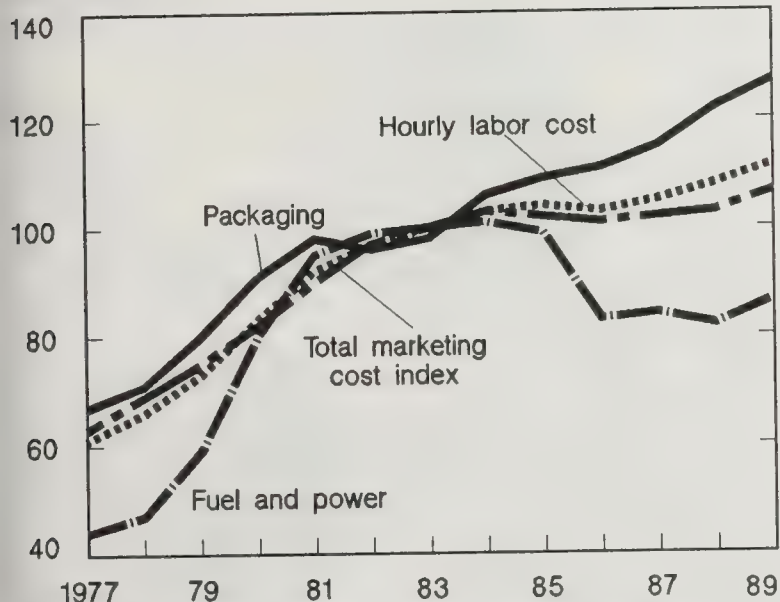
Food Marketing Costs

The marketing bill, the largest share of the food dollar, has risen faster than the farm value of raw foodstuffs, reflecting the rising cost of labor, packaging, and other inputs. Labor costs were responsible for over a third of the food dollar. Farm value, as a percentage of the total food dollar, is lower for the away-from-home market due to added costs of preparing and serving food.

Chart 138

Food processing, wholesaling, and retailing costs

% of 1982-84

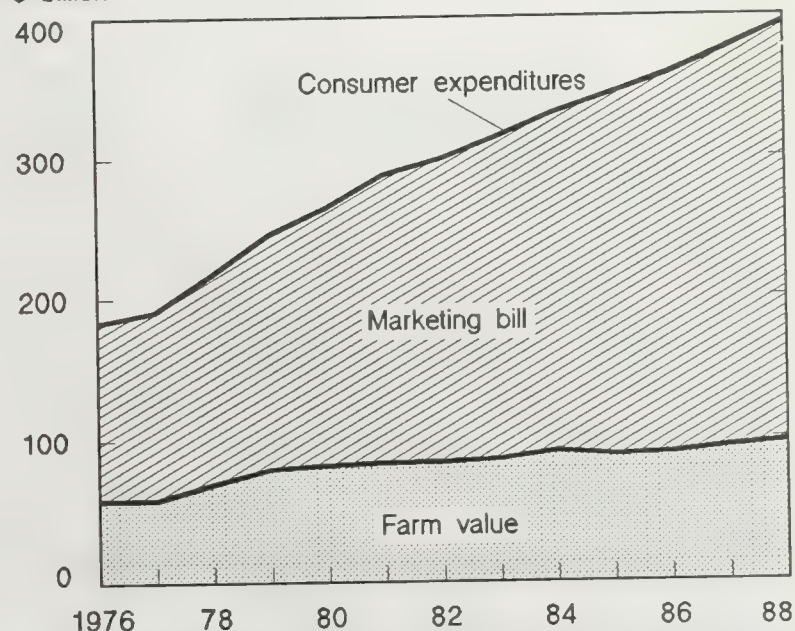


1989 forecast. The marketing cost index measures changes in worker wages, salaries, and supplemental benefits, and prices of purchased inputs such as packaging materials and fuel and power.

Chart 139

Marketing bill, farm value, and consumer expenditures for farm foods

\$ billion



Data for domestically produced farm foods purchased by civilian consumers for consumption both at home and away from home.

Chart 140

What a dollar spent on food paid for in 1988

Farm value 25 ¢

Marketing bill:

Packaging 8 ¢

Transportation 4.5 ¢

Before-tax profits 3.0 ¢

Fuel and power 3.5 ¢

Depreciation 4.5 ¢

Advertising 4.5 ¢

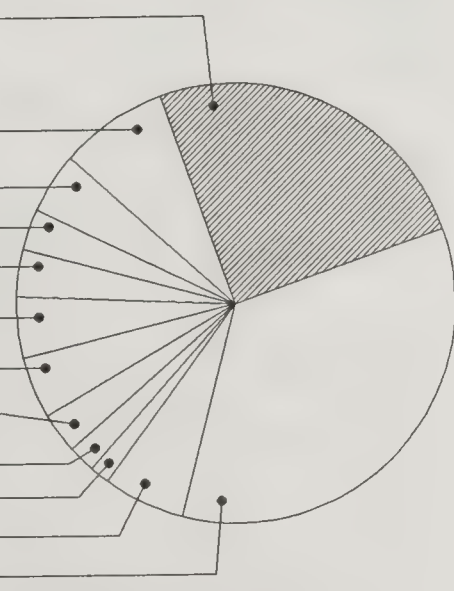
Rent 3 ¢

Interest (net) 2 ¢

Repairs 1.5 ¢

Other 6 ¢

Labor 34.5 ¢



Other costs include property taxes and insurance, accounting and professional services, promotion, bad debts, and miscellaneous items.

Chart 141

Where the food dollar goes at home and away

At home:

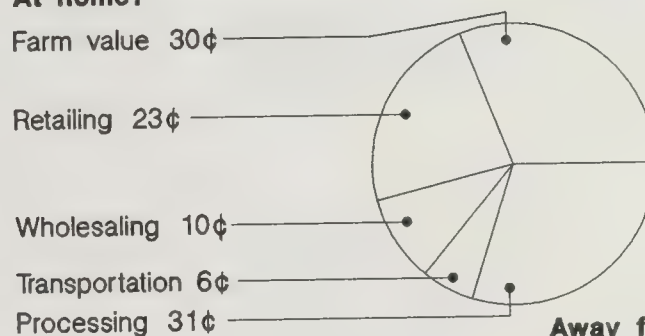
Farm value 30¢

Retailing 23¢

Wholesaling 10¢

Transportation 6¢

Processing 31¢



Away from home:

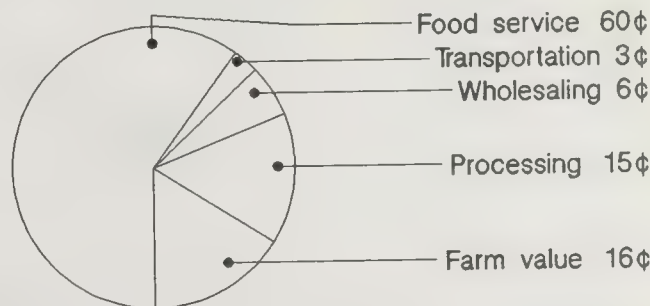
Food service 60¢

Transportation 3¢

Wholesaling 6¢

Processing 15¢

Farm value 16¢



1988 data.

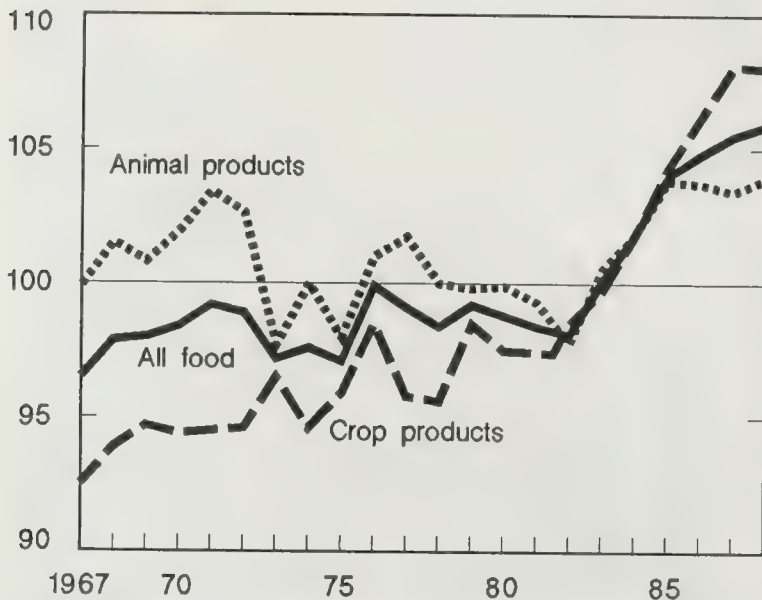
Food Consumption

The average American consumed more poultry, fish, lowfat milk, yogurt, cheese, fruits, vegetables, grain products (pasta, rice, breakfast cereals), fats and oils, and sweeteners, and less red meat, whole milk, and eggs in 1988 than in 1982-84.

Chart 142

Per capita consumption of food

% of 1982-84

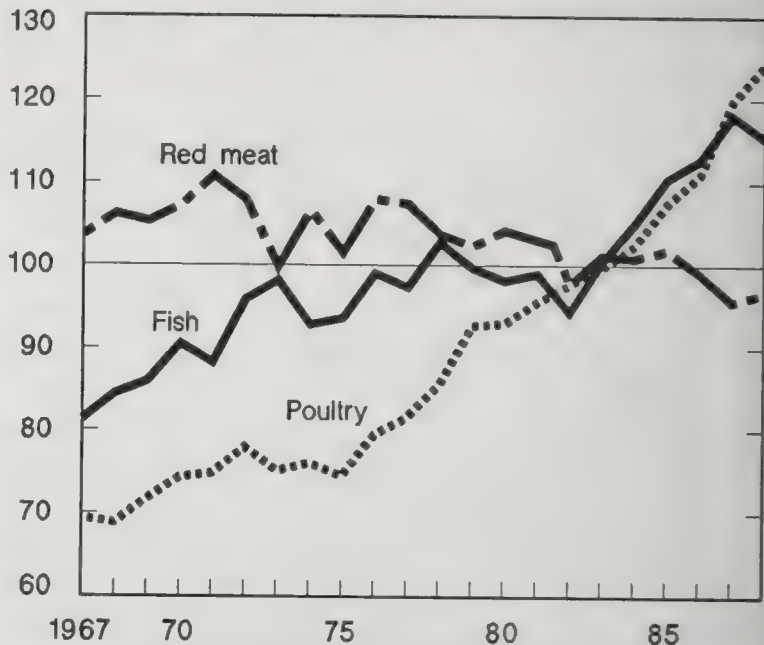


The price-weighted per capita food consumption index measures quantity changes, but also reflects certain changes in the quality of foods consumed, such as the shift from processed vegetables to fresh vegetables.

Chart 143

Per capita consumption of red meat, poultry, and fish

% of 1982-84

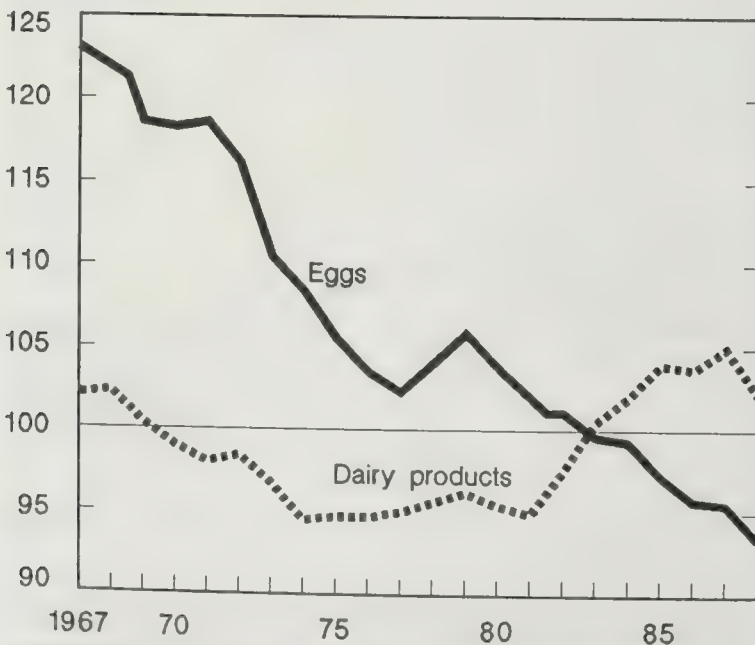


Indexes based on pounds consumed per person, boneless trimmed equivalent.

Chart 144

Per capita consumption of eggs and dairy products

% of 1982-84

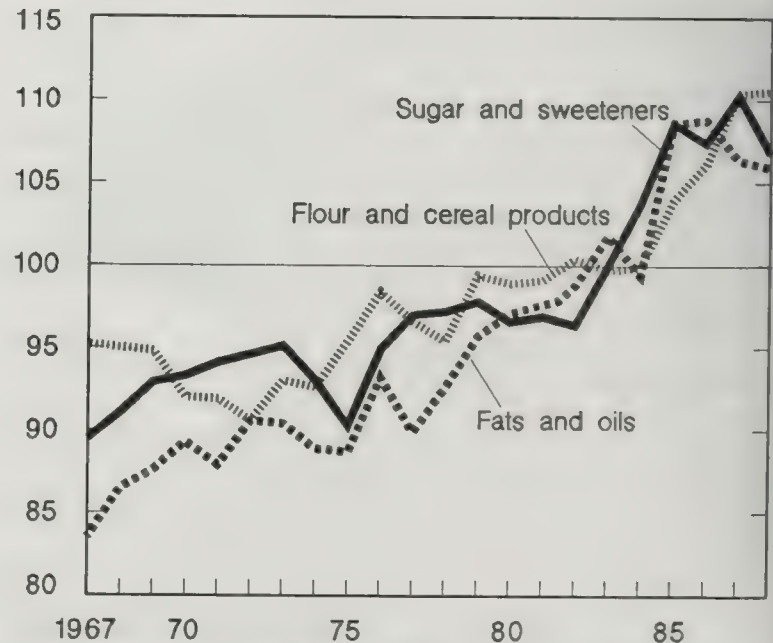


Indexes based on pounds consumed. Milk equivalent for all dairy products.

Chart 145

Per capita consumption of selected processed products

% of 1982-84

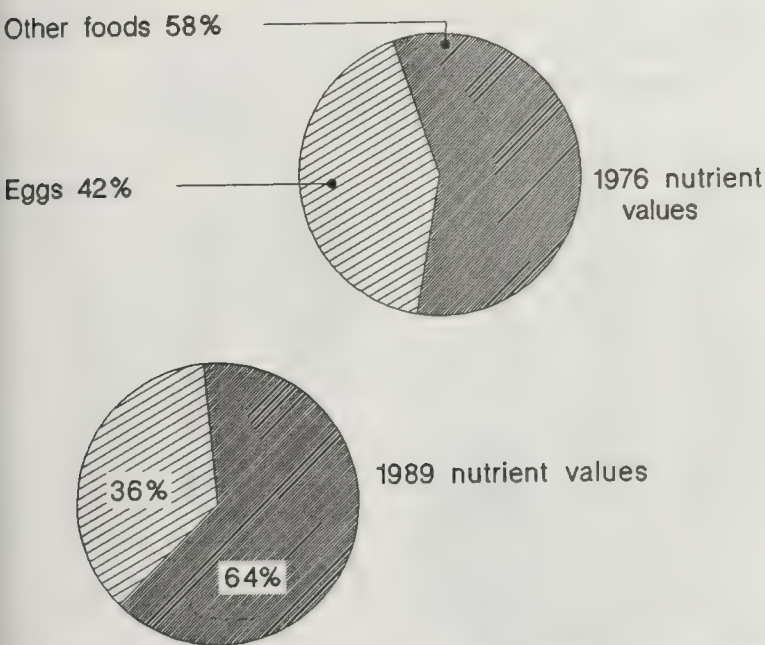


These indexes measure quantity changes only.

Women's Diet

New research shows a lower value for cholesterol in eggs in 1989 than in 1976. Values of some other nutrients changed as well. The new value for eggs reduces the proportion of women's intake of cholesterol that comes from eggs. Beef has new nutrient values which result from more fat being removed at the retail level. Proportions of fatty acids in dietary oils vary by type of oil.

Chart 146
Effect of new nutrient values on eggs' share of women's cholesterol intake



Note: Includes eggs eaten separately and those eaten as part of a mixture, such as custard. Source: Continuing Survey of Food Intakes by Individuals, 4 days, 1985.

Table 1
Changes in the nutrient value of one large egg

Item	1976	1989
Cholesterol(mg)	274	213
Iron(mg)	1.04	.72
Fat(g)	5.58	5.01
Vitamin B ₁₂ (mcg)	.77	.50

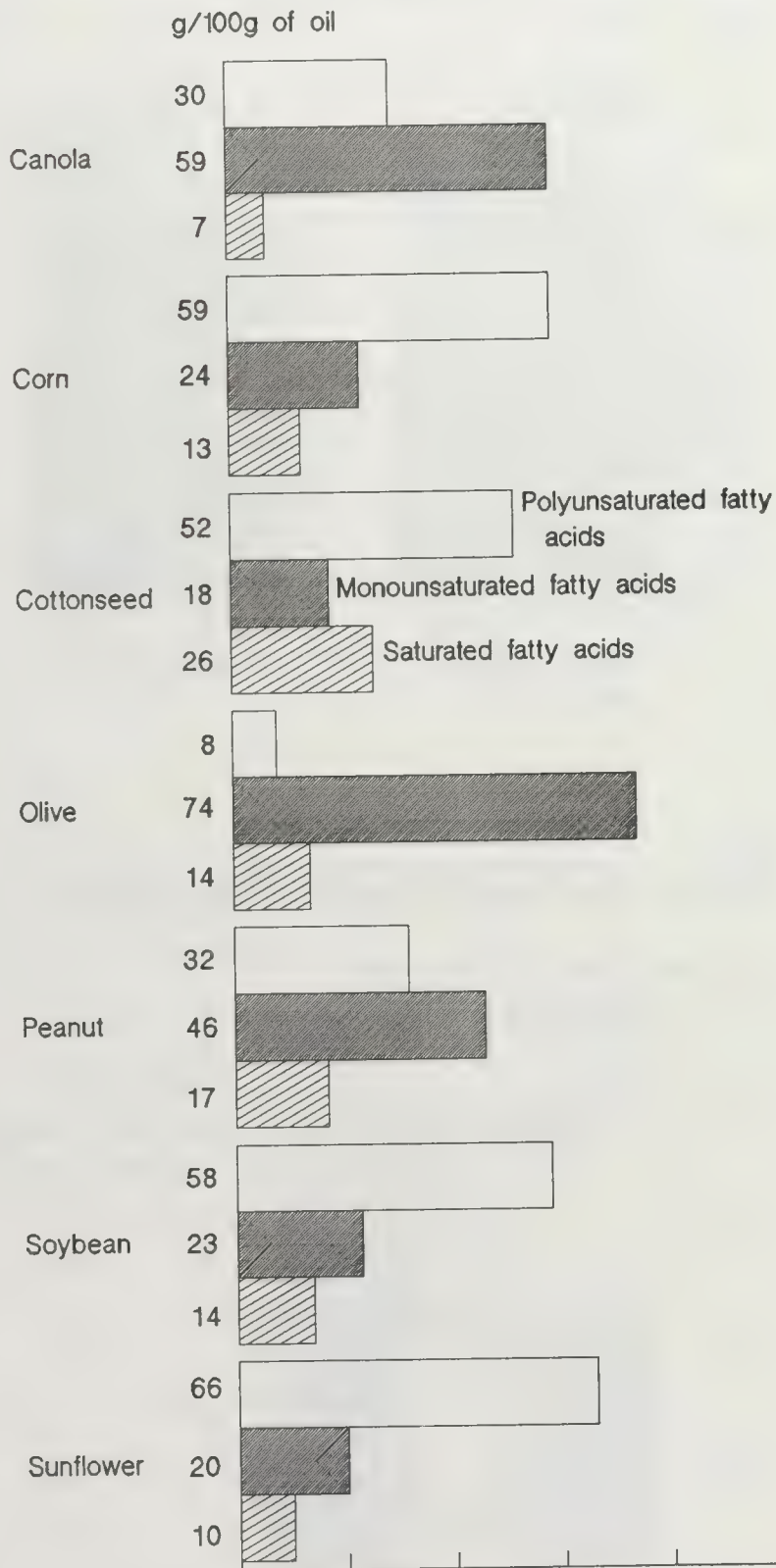
Source: Agriculture Handbook No. 8-1, 1976; Agriculture Handbook No. 8, 1989 Supplement.

Table 2
Changes in nutrient values of 100g of beef resulting from fat trim changes at the retail level

Item	1986 1/2" trim	1989 1/4" trim	1989 0" trim
Water(g)	57	59	64
Food energy(kcal)	243	229	171
Protein(g)	27	27	29
Total lipid(g)	14	13	5

Eye of round, separable lean and fat, roasted. Source: National Nutrient Data Bank Conference, June 1989.

Chart 147
Comparison of dietary oils



Source: Agriculture Handbook No. 8-4, 1989 Supplement.

Women's Diet

American women are eating more meat and grain mixtures, which are foods made by combining ingredients from major food groups. Examples include beef stew, stir-fry, pizza, burritos, pasta salads, and frozen plate meals. The major food groups represented by food mixture ingredients are meat, poultry, and fish products; grain products; vegetables; and milk, cheese, and yogurt.

Chart 148

Meat, poultry, and fish products and grain products consumed by women

Grams per day

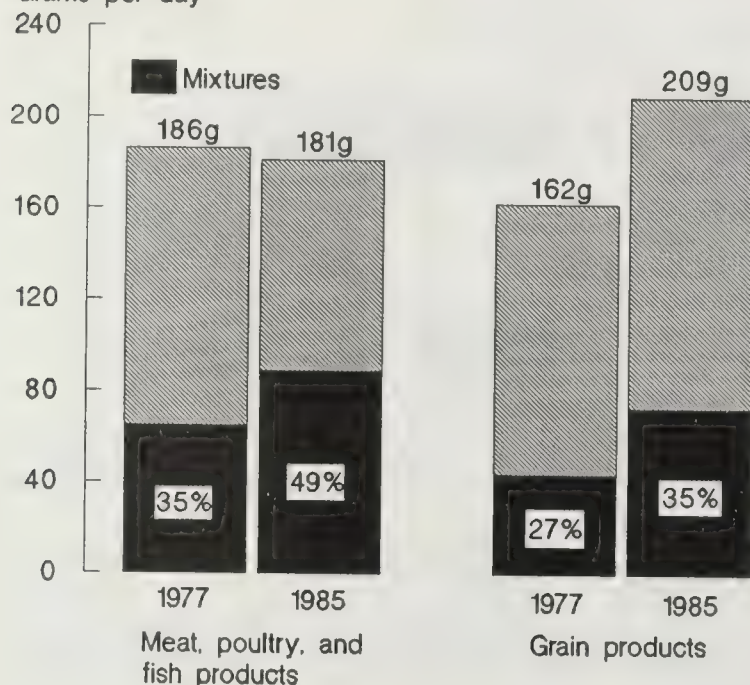


Chart 149

Major food groups in mixtures consumed by women, 1985

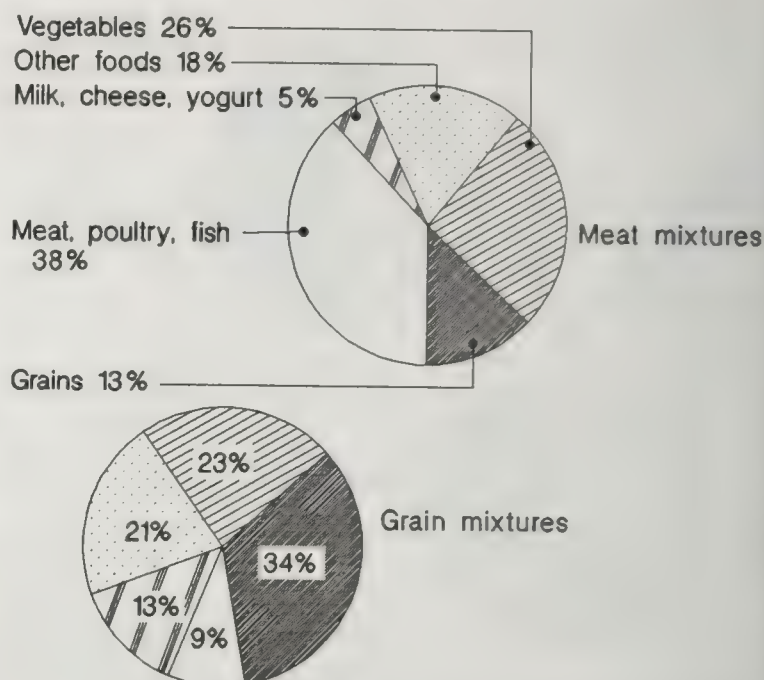
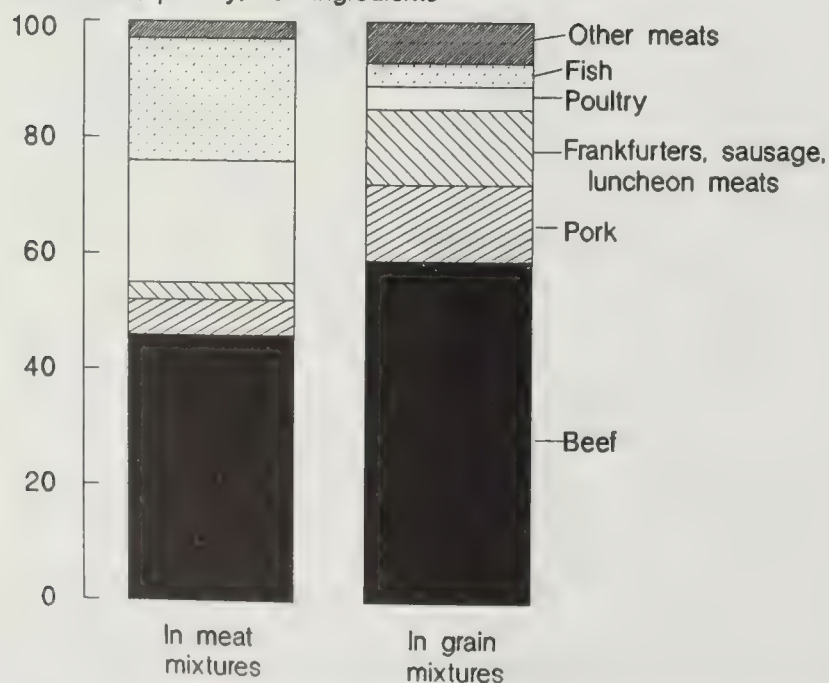


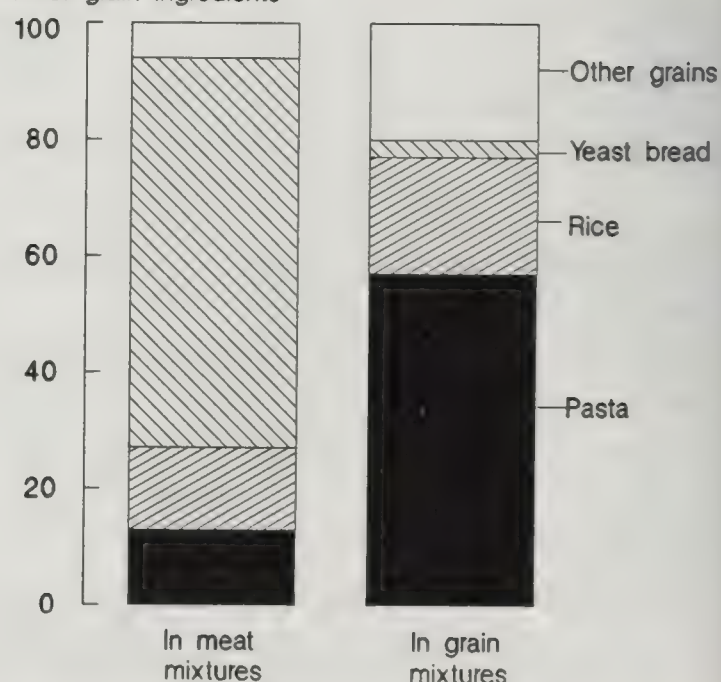
Chart 150

Specific Ingredients in mixtures consumed by women, 1985

% of meat, poultry, fish ingredients



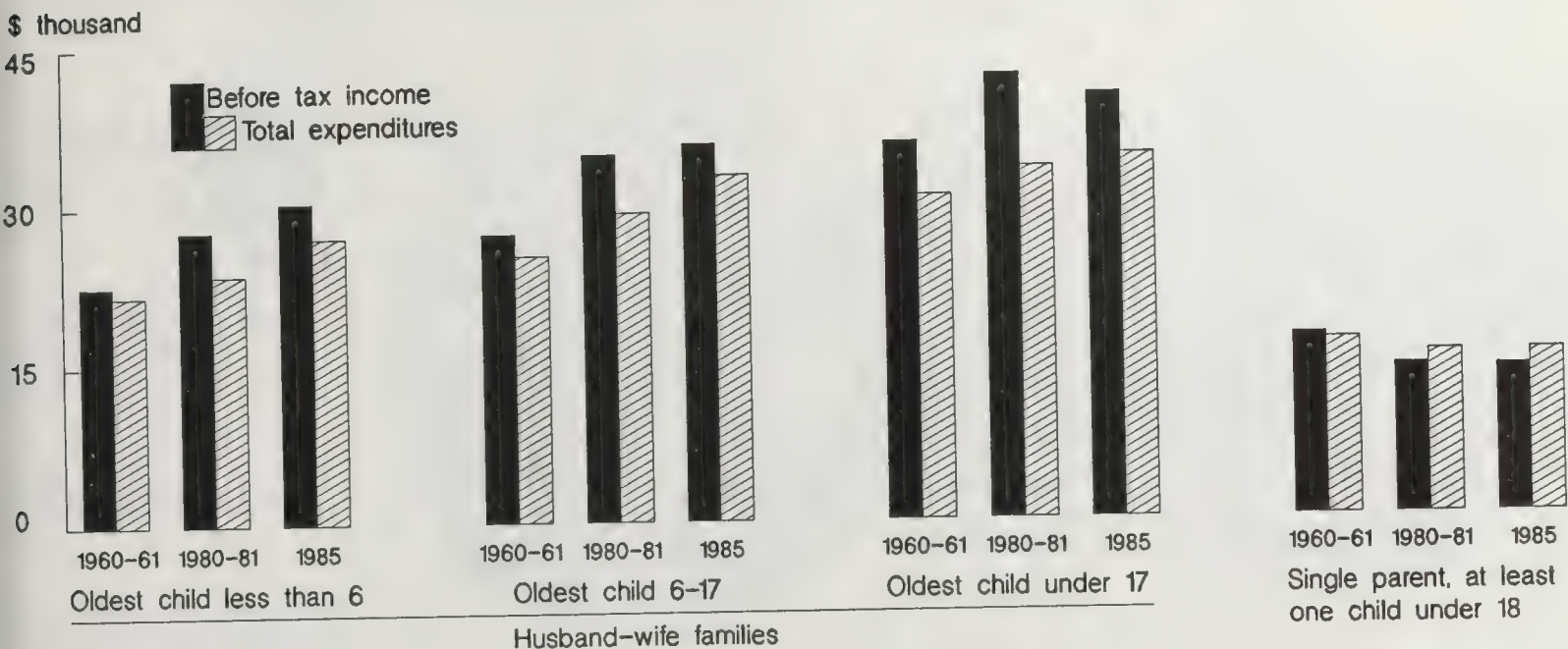
% of grain ingredients



Family Economics

Real income and expenditures for single-parent families have declined since 1960-61. Prices for food and transportation increased by over 90 percent, and housing prices increased by 116 percent since 1977. Housing and transportation now comprise higher shares of the household budget than in 1960-61.

Chart 151
Real income and expenditures for families with children



Consumer Expenditure Survey data. Source: Bureau of Labor Statistics.

Chart 152
Changes in consumer prices for food, housing, and transportation

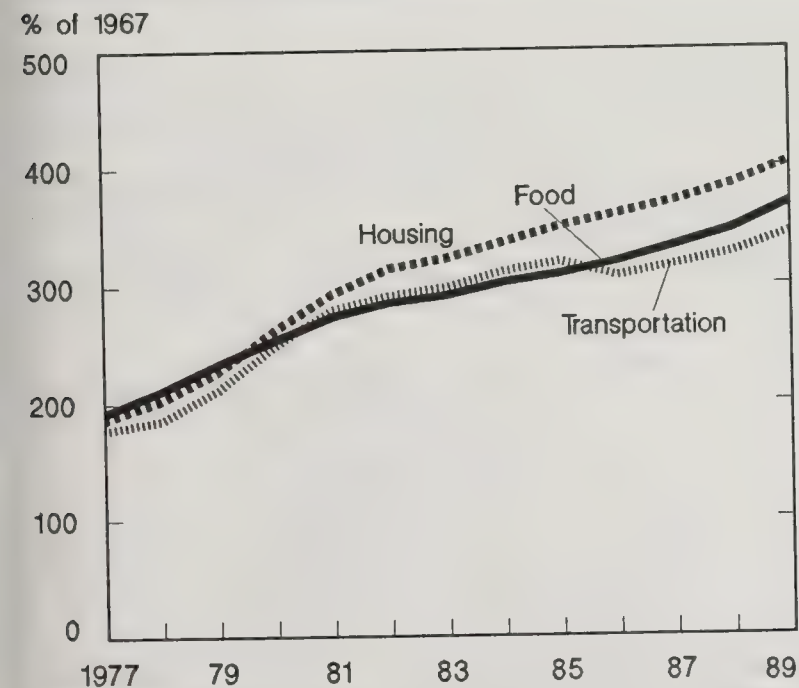
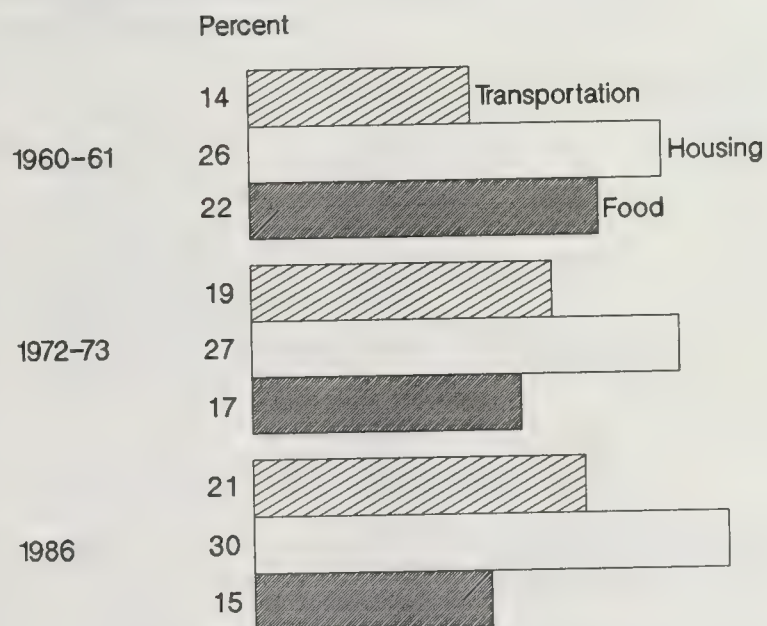


Chart 153
Changes in household budget shares, all households



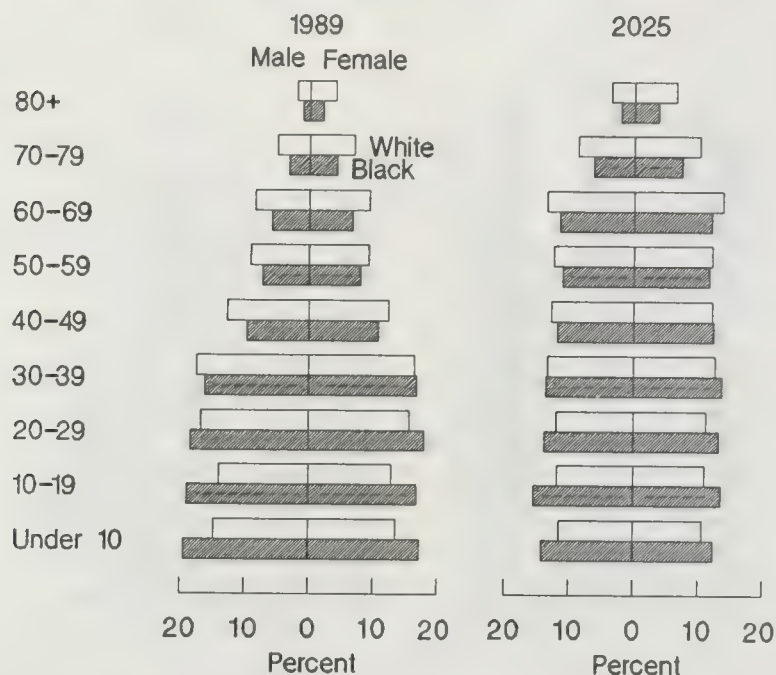
Consumer Expenditure Survey data. Source: Bureau of Labor Statistics.

Family Economics

Fifty-eight percent of the population of white females and 73 percent of black males were under age 40 in 1989; the population will be distributed more evenly among age groups under 70 by 2025. Elderly individuals depend on Social Security and their personal assets for about 75 percent of their income. The proportion of unmarried elderly living alone has nearly doubled since 1960.

Chart 154

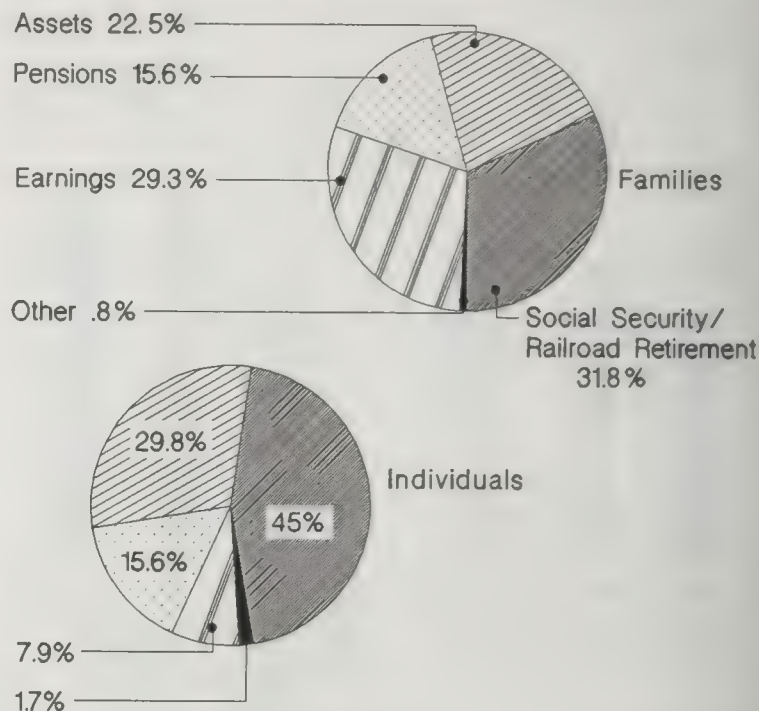
Population by age, sex, and race



Source: Bureau of the Census.

Chart 155

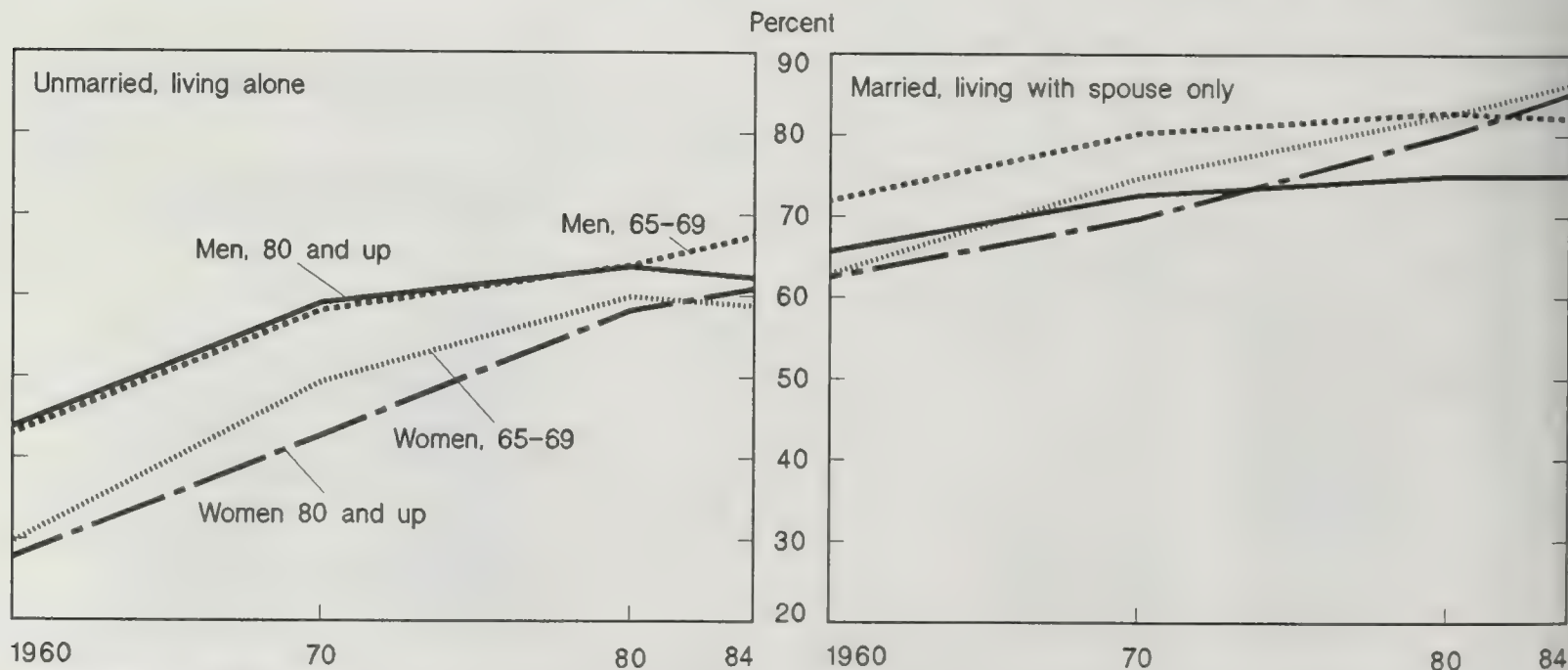
Income sources of the elderly



1985 data. Source: Bureau of the Census.

Chart 156

Living arrangements of the elderly

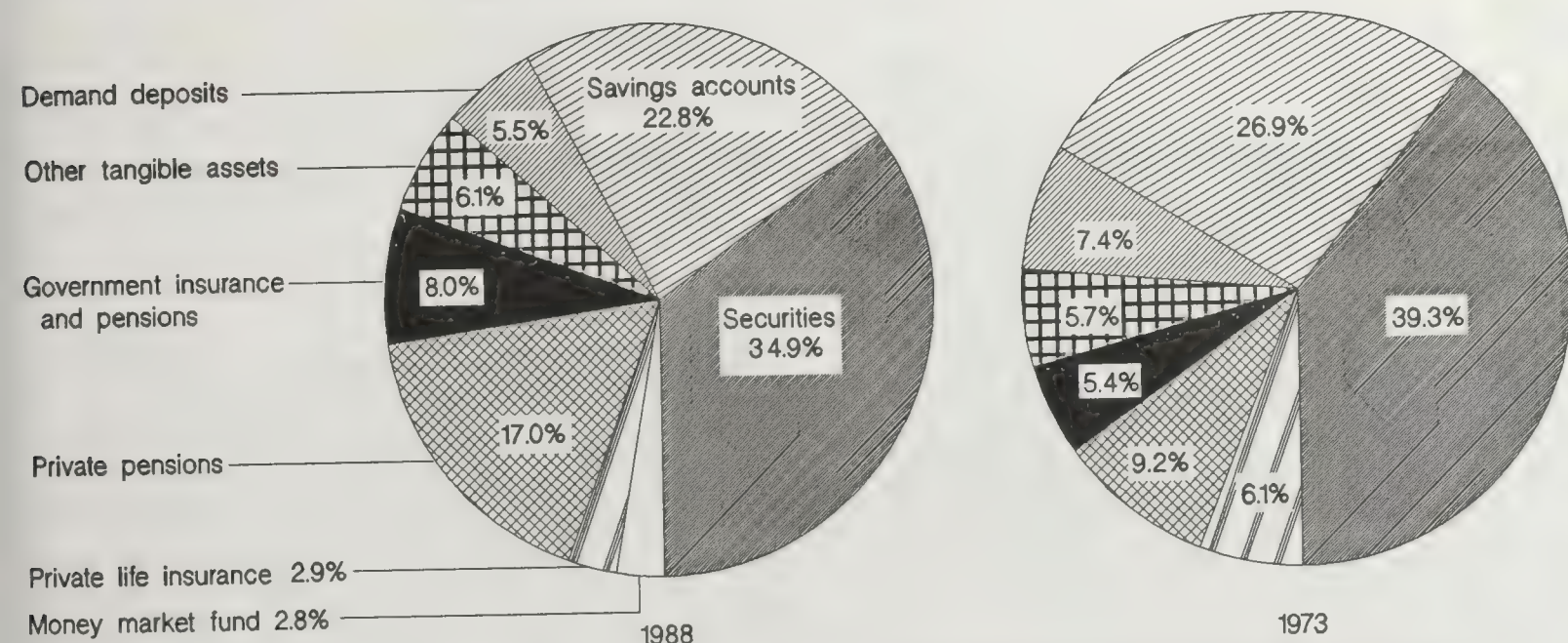


Source: Congressional Budget Office.

Family Economics

Individuals held a higher proportion of assets in private pensions in 1988 than in 1973. Interest rates on consumer loans changed little in 1988, although the prime rate increased by 1 percentage point. Additional education by white husbands increases family income more than that by white wives and black husbands or wives.

Chart 157
Distribution of financial assets



Other tangible assets include residential and nonresidential fixed assets, consumer durables, and inventories. 1973 money market funds were less than 1 percent.
Source: Federal Reserve Board.

Chart 158
Consumer loan rates

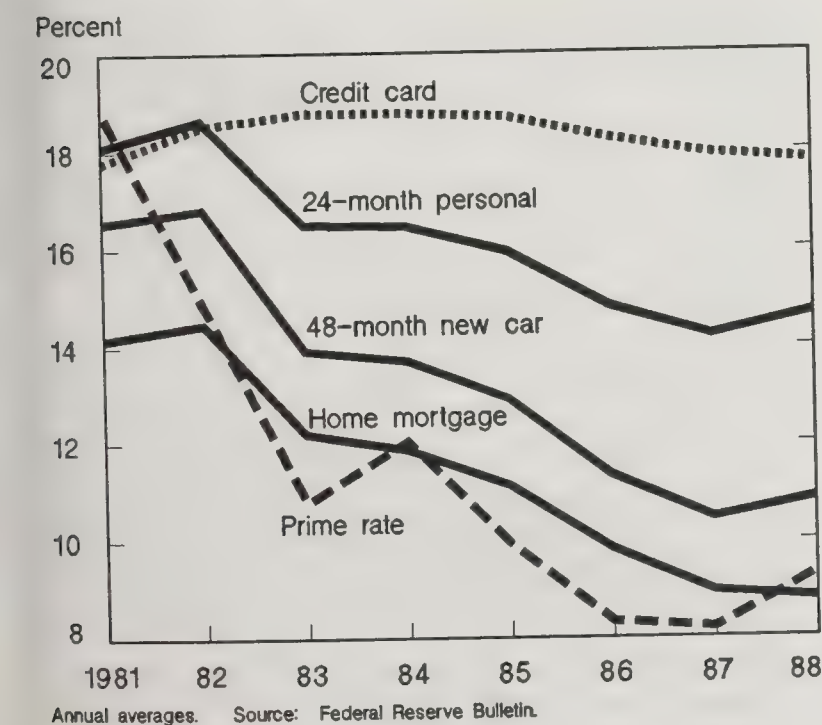
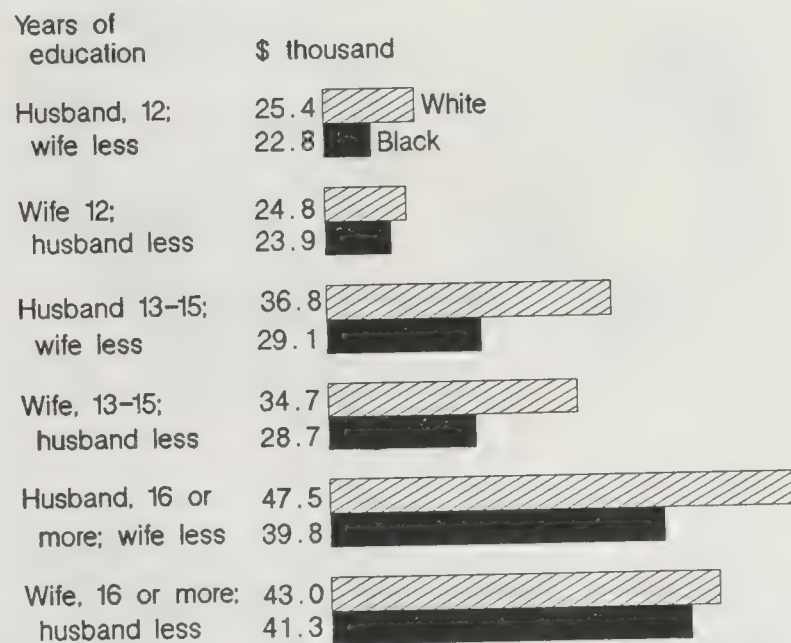


Chart 159
Family income by joint husband-wife educational level



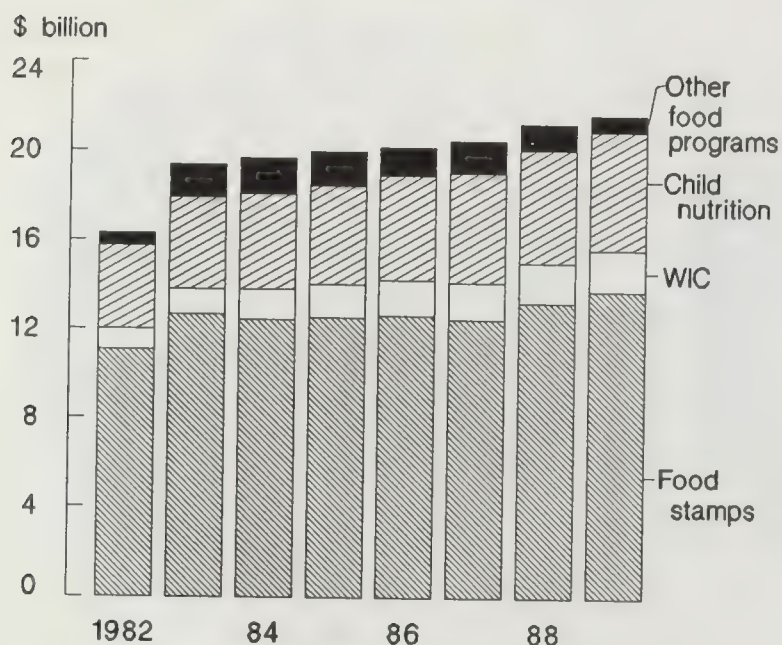
1988 data. Median income. Source: Bureau of the Census.

Food Assistance

Expenditures for the USDA Food Assistance Programs and direct benefits increased about 33 percent from 1982 to 1989. The number of Food Stamp beneficiaries has been trending down. Sixty-four percent of 1989 Food Assistance Program expenditures were for the Food Stamp Program. Food Stamp Program expenditures vary widely by State. WIC Program expenditures increased from 5.8 percent of the total in 1982 to 8.7 percent in 1989.

Chart 160

USDA costs for food assistance

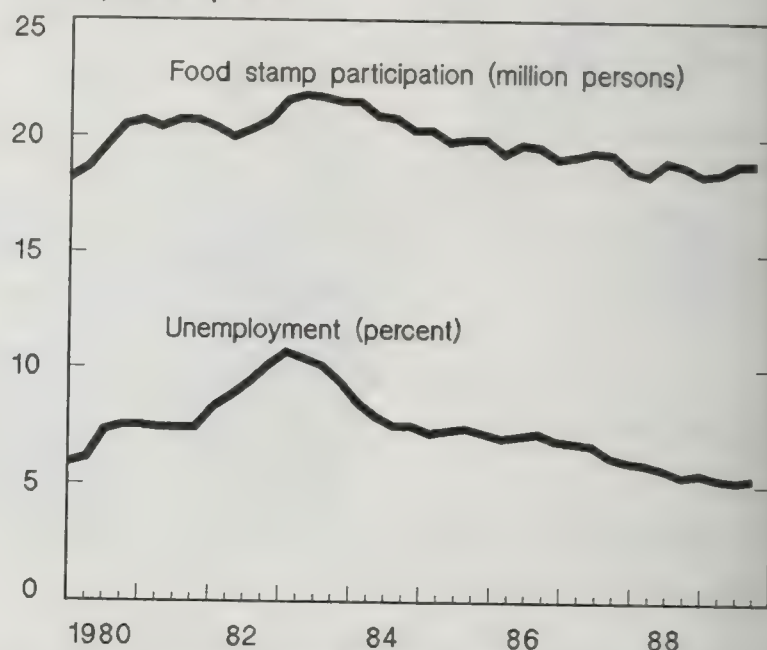


1989 estimated. Fiscal years. Other programs include administrative costs and surplus commodities. Food stamps include cash assistance for Puerto Rico. WIC is Women, Infants, and Children Program.

Chart 161

Unemployment rate and participation in the Food Stamp Program

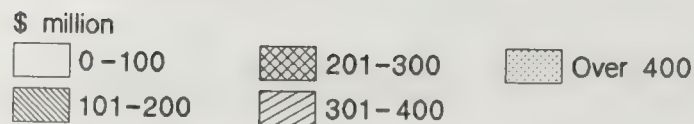
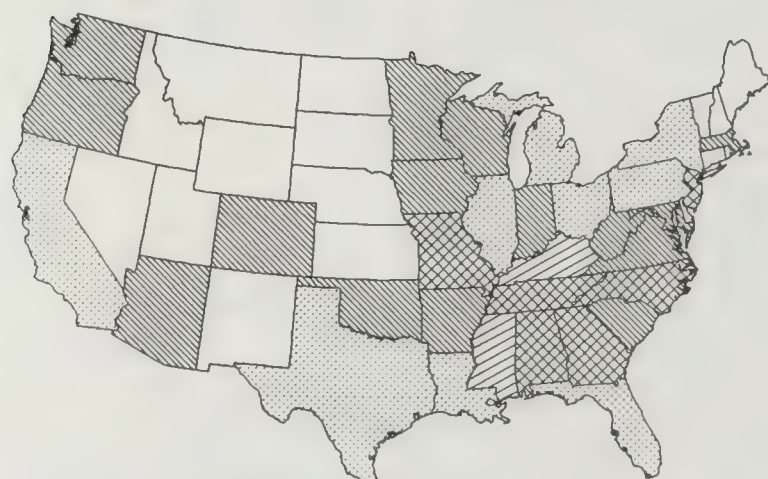
Million persons/percent



1989 estimated. Seasonally adjusted fiscal year data.

Chart 162

Expenditures for food assistance for the Food Stamp Program by State, 1988

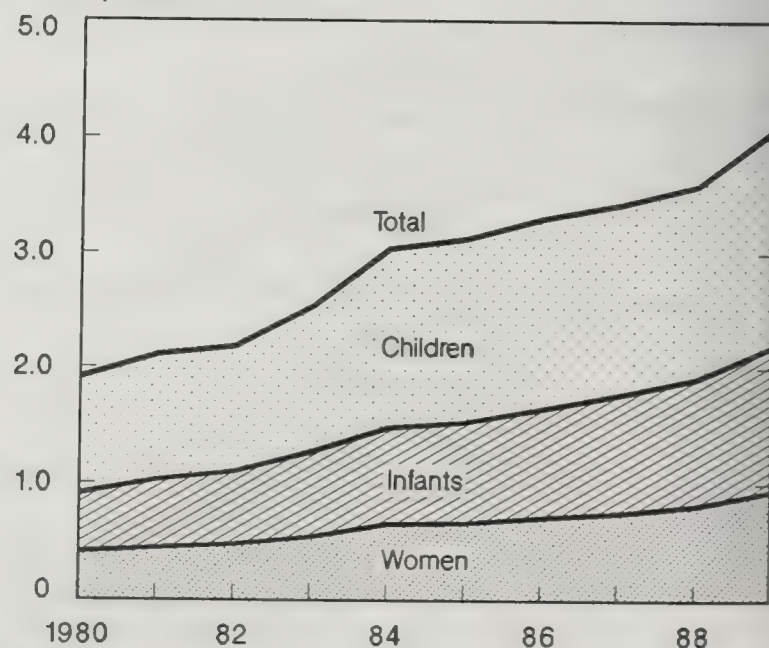


1987 fiscal year data.

Chart 163

Participants in the WIC Program

Million persons



1989 estimated. Fiscal years.

Child Nutrition and Food Distribution

More children in the National School Lunch and Breakfast Programs paid full price for their meals in 1989. Fewer children have received meals free since 1980. Meals served to children in the Child Care Food Program reached a new high. About 2.5 million meals were served under the program in adult day care centers for the functionally impaired.

Chart 164
Children in the National School Lunch Program

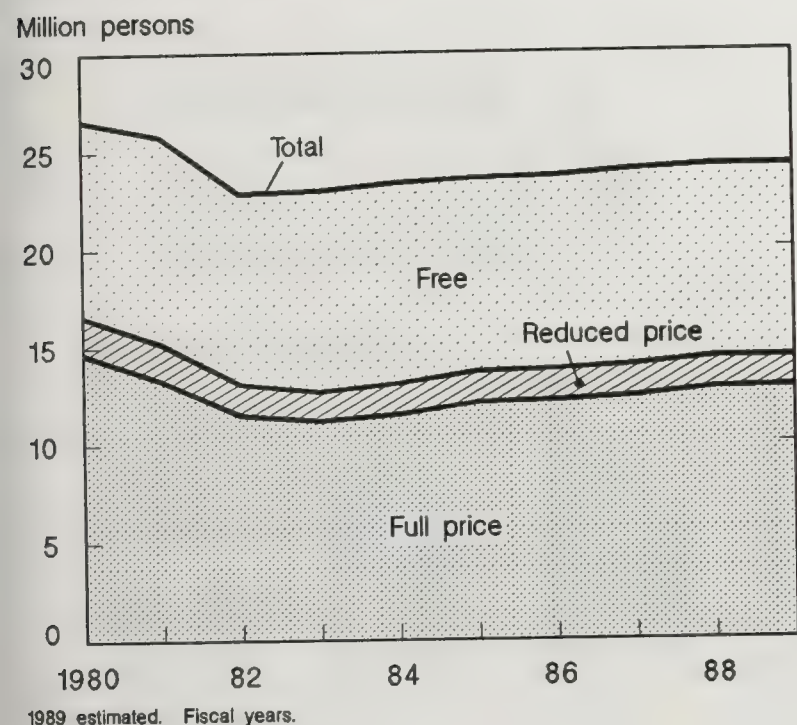


Chart 165
Children in the School Breakfast Program

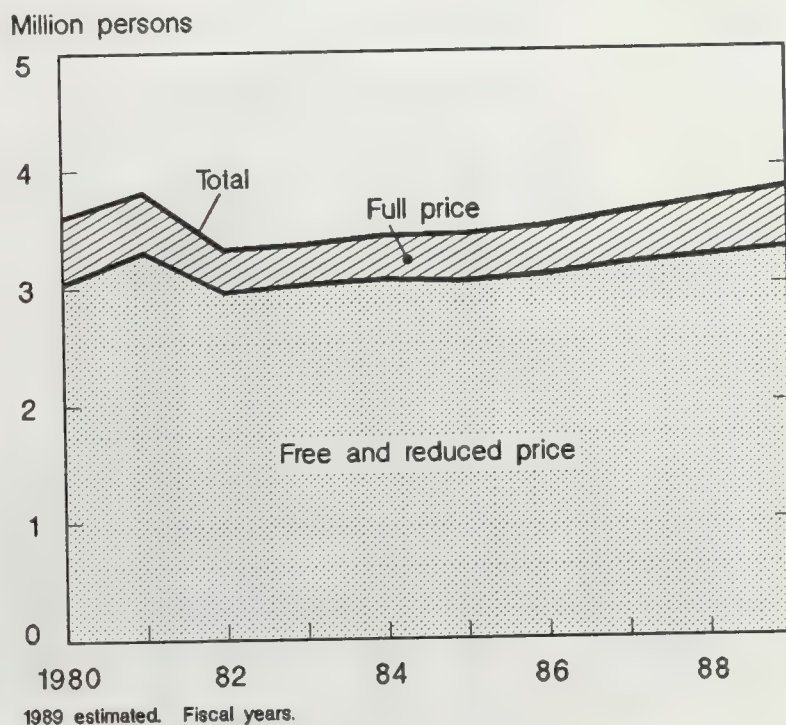


Chart 166
Meals served in the Child Care Food Program

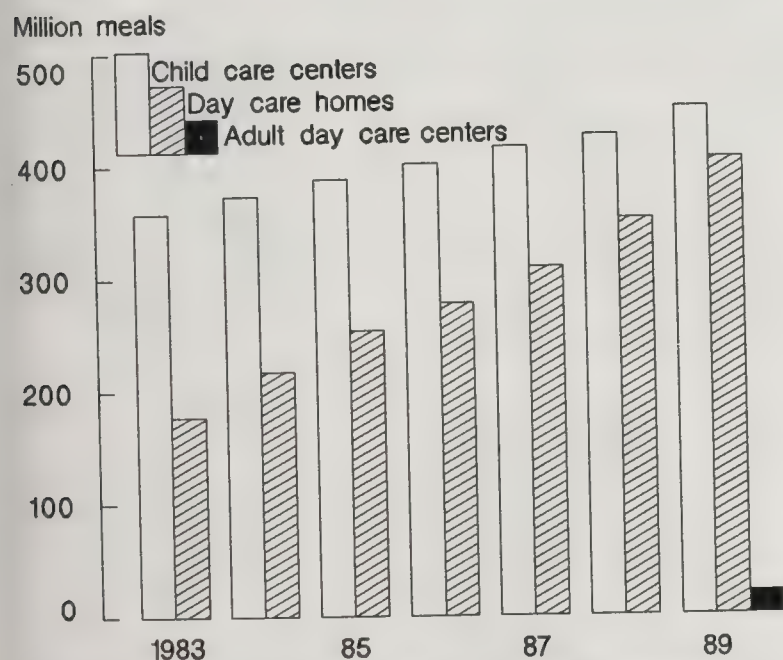
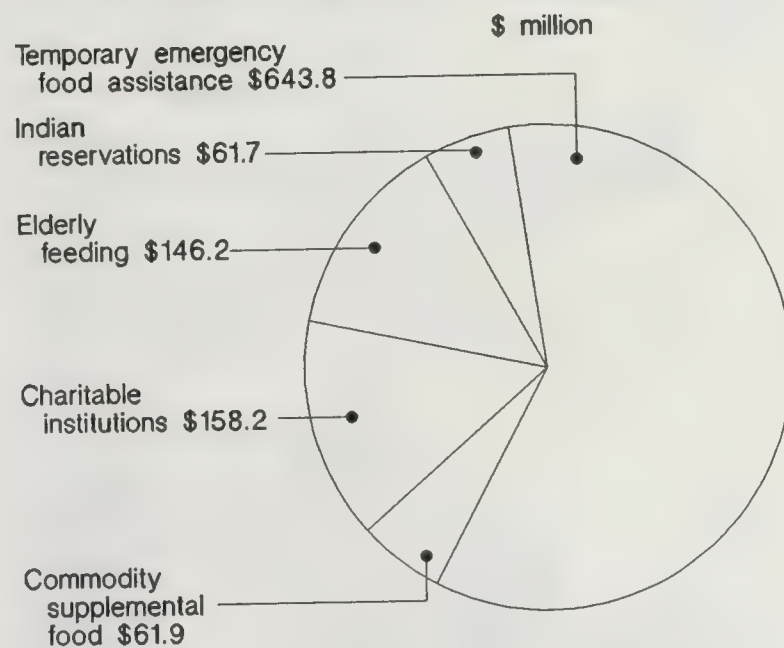


Chart 167
Food donation costs, 1988



Preliminary fiscal year data. Excludes Child Nutrition Programs.

Producer Subsidy Equivalents

Japan and Korea provided the highest levels of support for their producers followed by the EC, Canada, the United States, Taiwan, and Australia. U.S. agricultural producer assistance went mostly to grain and dairy producers. Producer subsidy equivalents (PSE's) measure levels of support (or taxation) provided to producers by domestic farm programs and agricultural trade barriers. PSE's report the value of government support as a percentage of producers' agricultural income (cash receipts plus direct payments).

Chart 168

Developed country annual producer subsidy equivalents averaged over major commodities

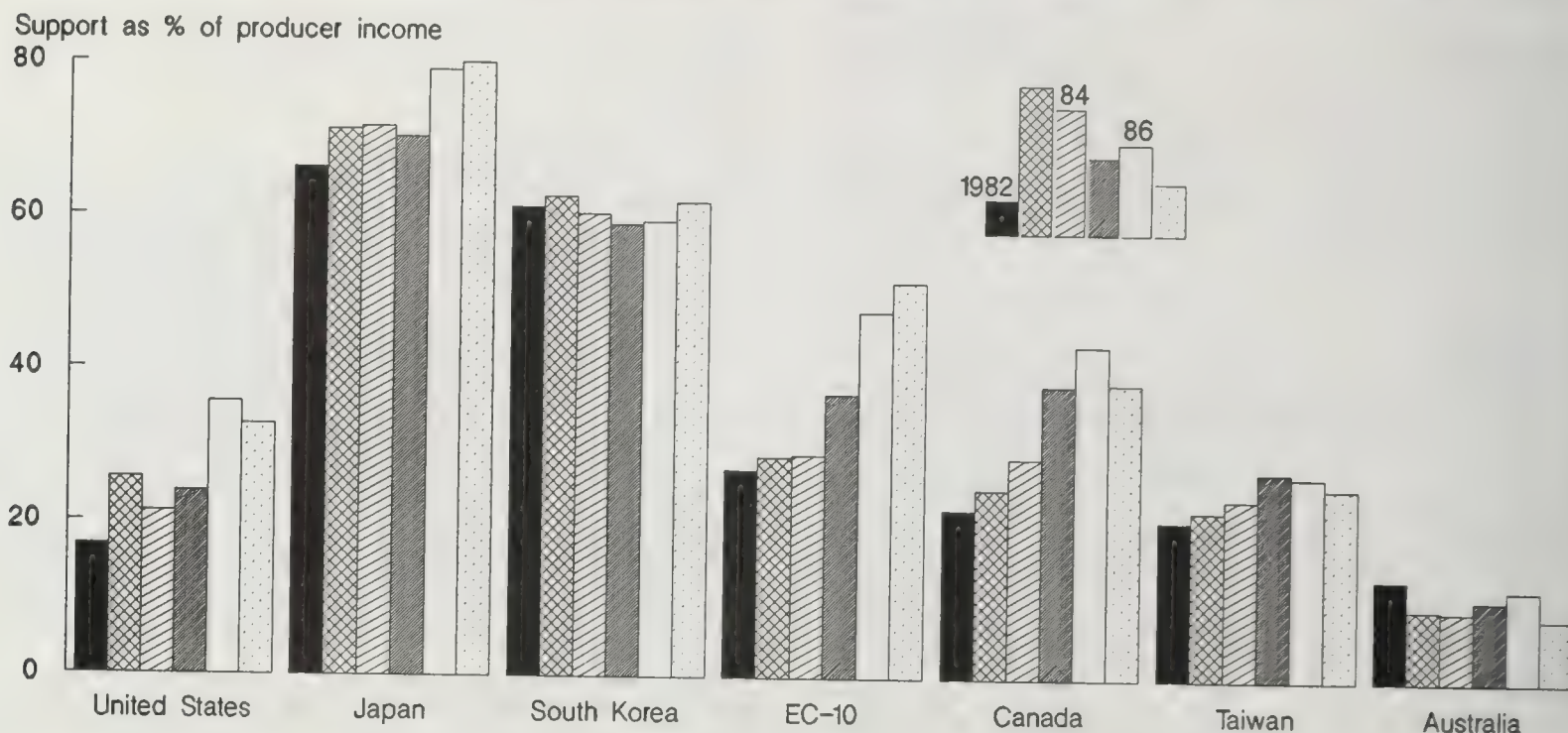


Chart 169

Sources of producer support in the United States by commodity groups, 1987

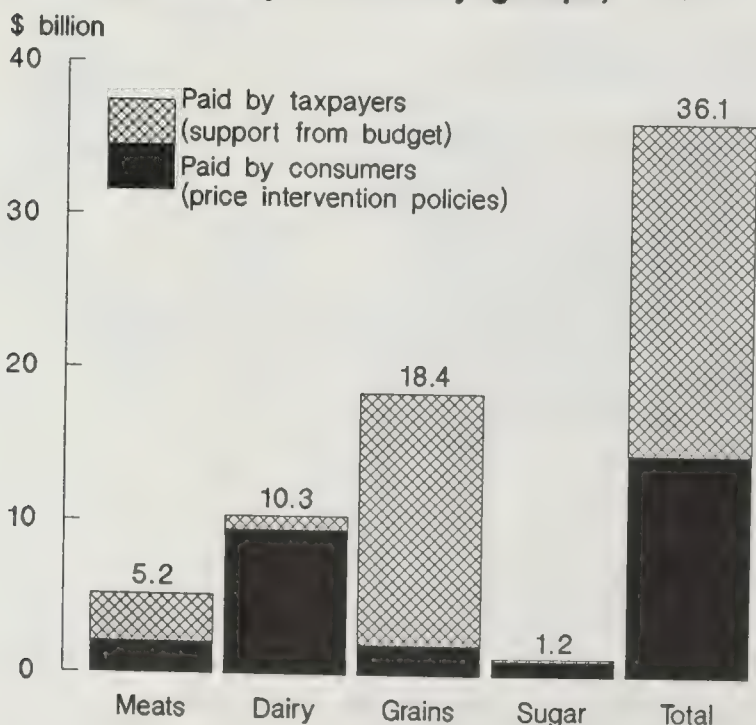
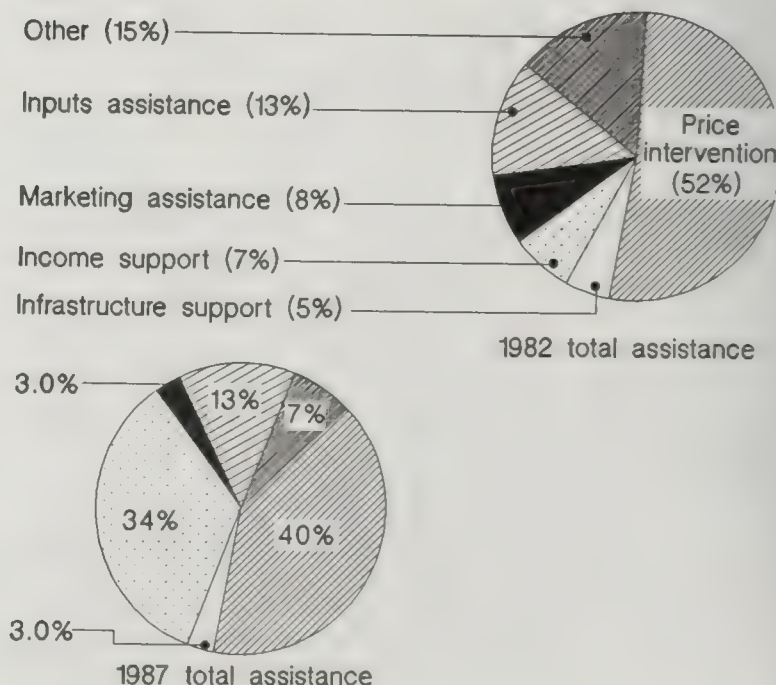


Chart 170

Distribution of U.S. assistance by type of assistance



World and U.S. Trade

World trade of semiprocessed products increased almost fourfold from the 1960's to the mid-1980's. Trade of low-value unprocessed commodities increased at a slower rate. U.S. exports of highly processed agricultural products doubled in volume from 1961 to 1986.

Chart 171

Value-weighted quantity indices of agricultural exports: World

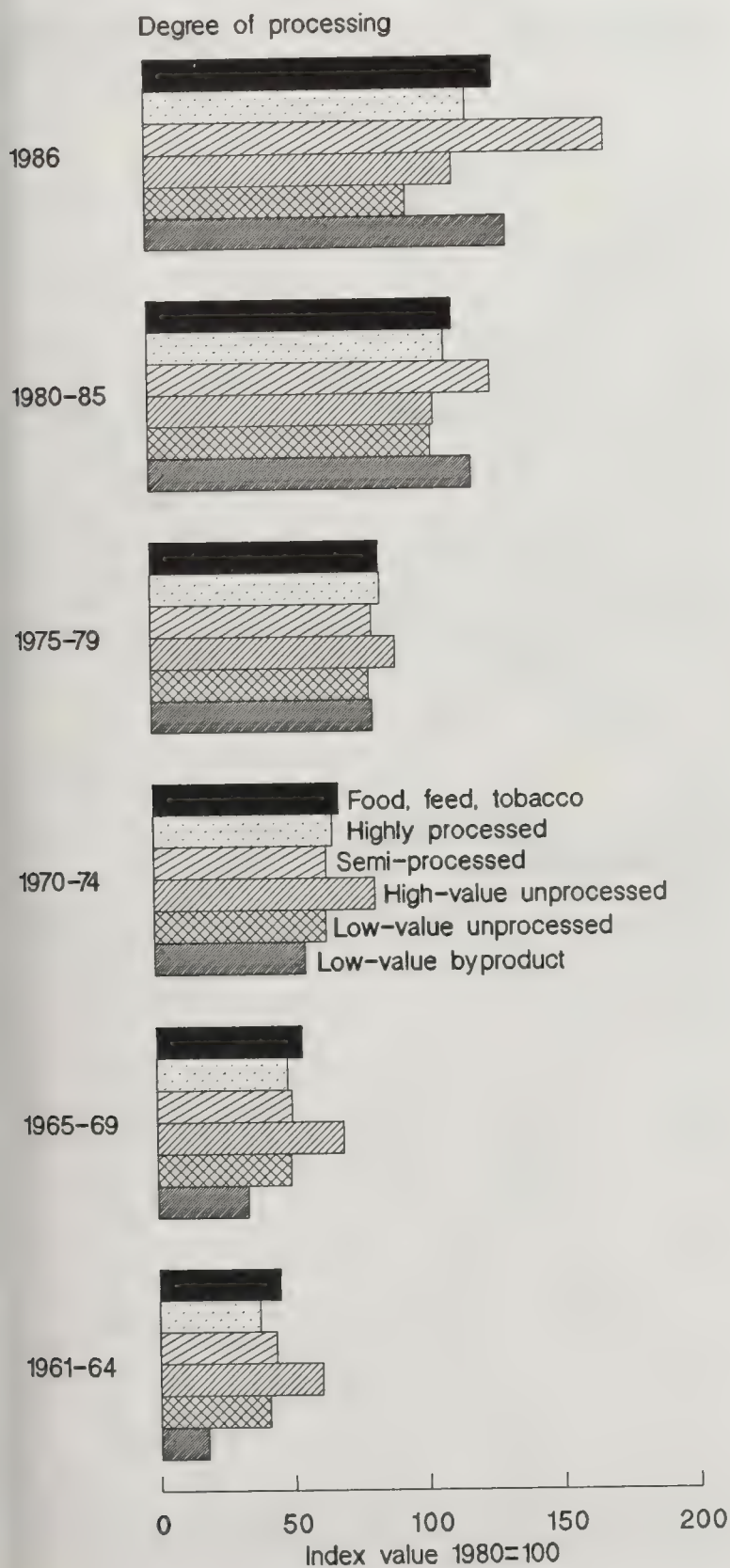
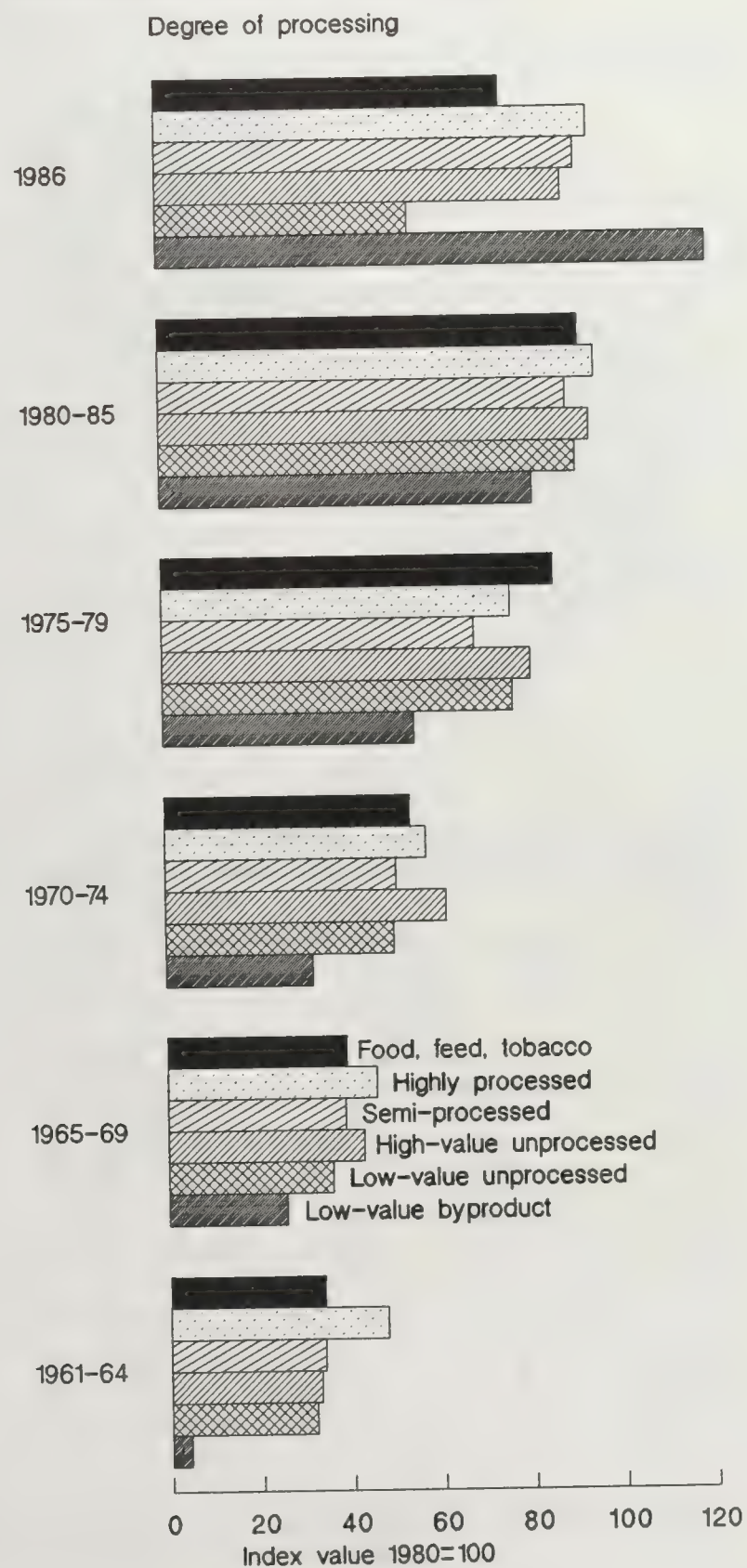


Chart 172

Value-weighted quantity indices of agricultural exports: United States



U.S. Trade

The most heavily indebted countries have had to use an increasing proportion of their available foreign exchange earnings to repay debt during the 1980's. U.S. export programs have helped many heavily indebted countries maintain needed food imports. The slowdown in capital formation in the most heavily indebted countries implies that incomes in these countries will rise slowly.

Chart 173

U.S. agricultural exports to indebted countries

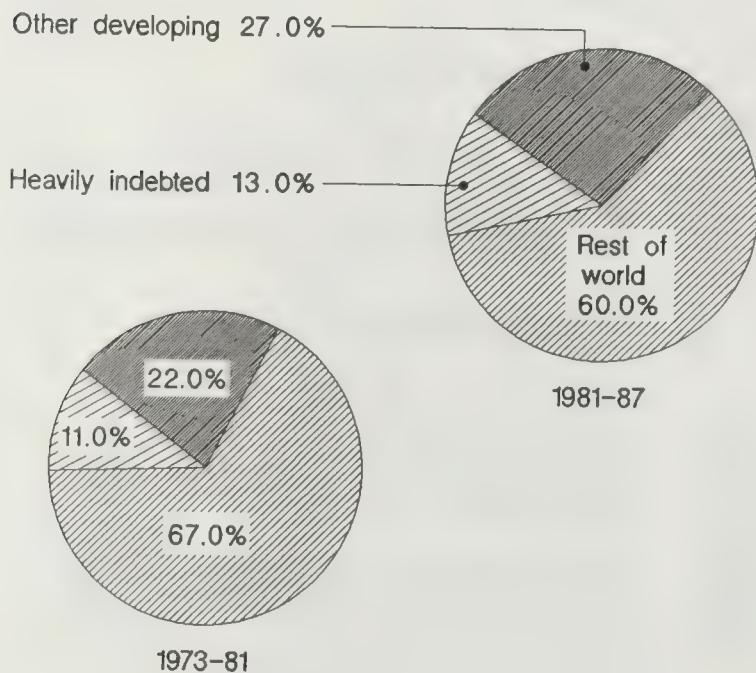
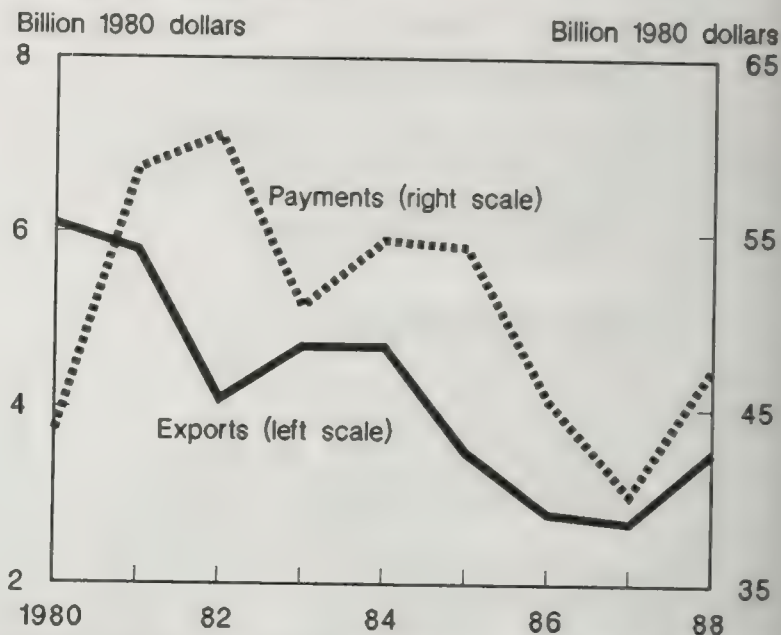


Chart 174

Debt service payments and U.S. agricultural exports to most heavily indebted countries



High debt-service payments in the 1980's forced the heavily indebted countries to cut back on agricultural imports, including those from the United States.

Chart 175

U.S. agricultural exports under Federal programs to most heavily indebted countries

Billion dollars

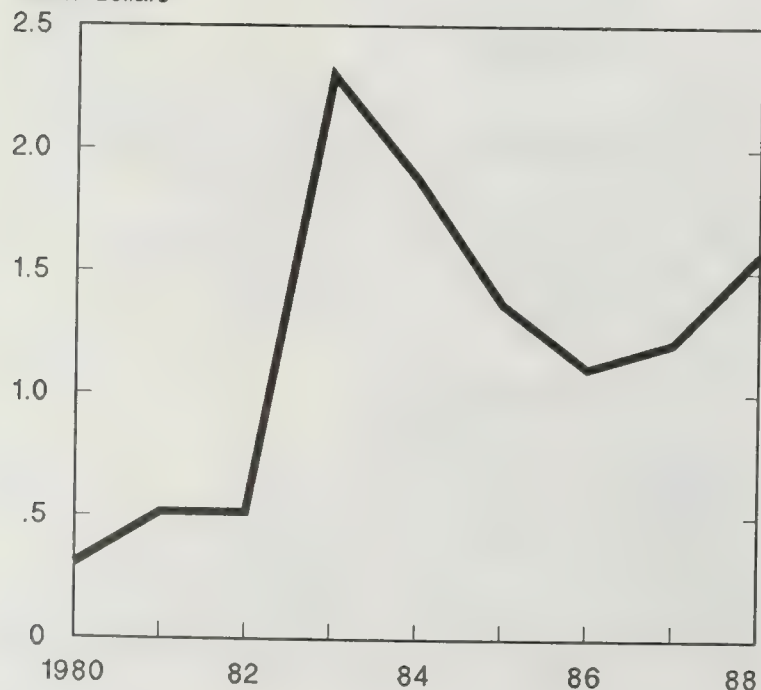
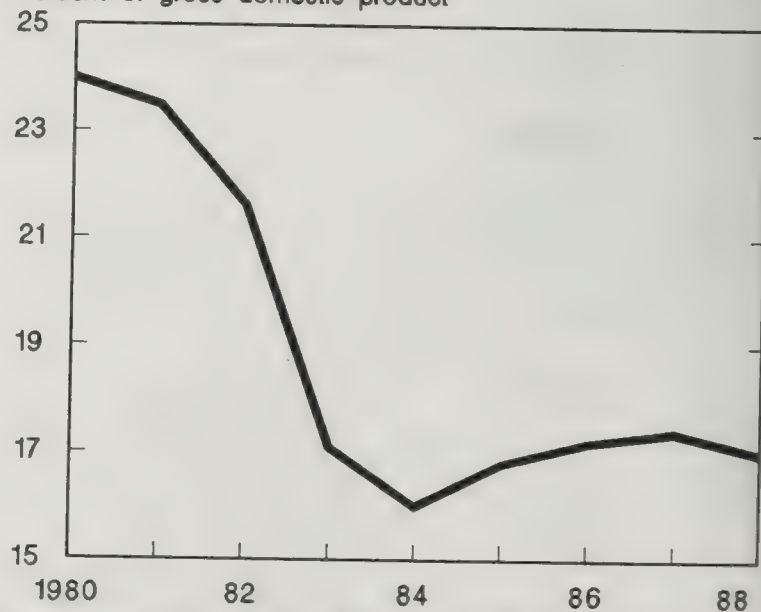


Chart 176

Capital formation in most heavily indebted countries

Percent of gross domestic product

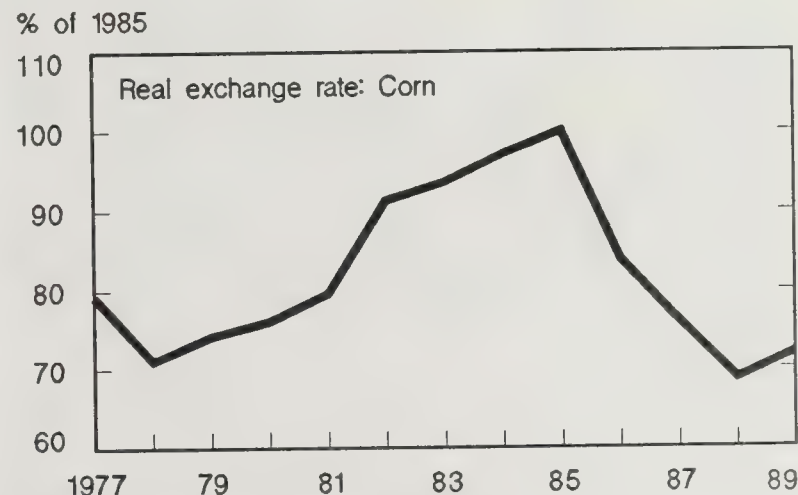
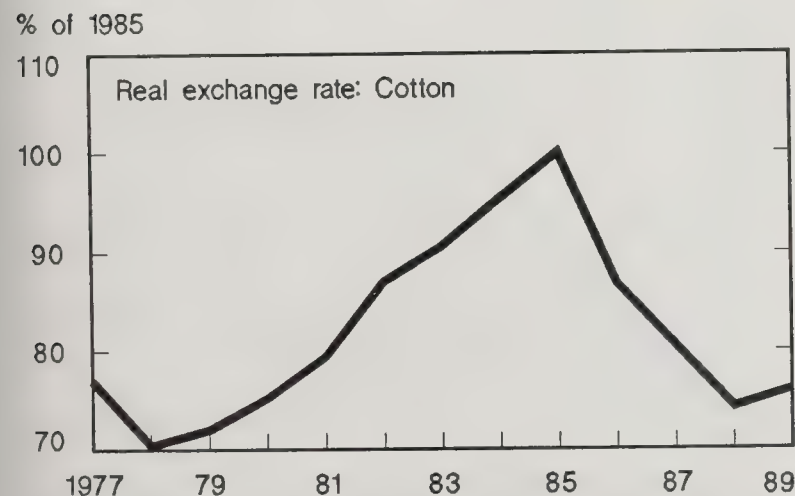
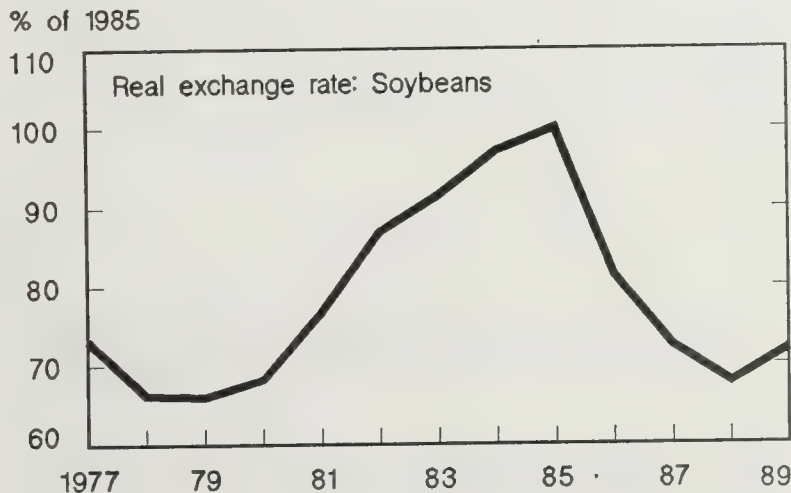
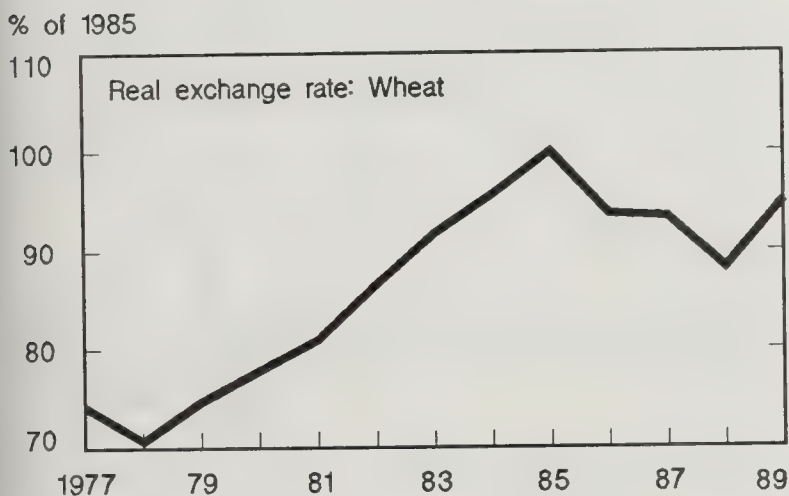
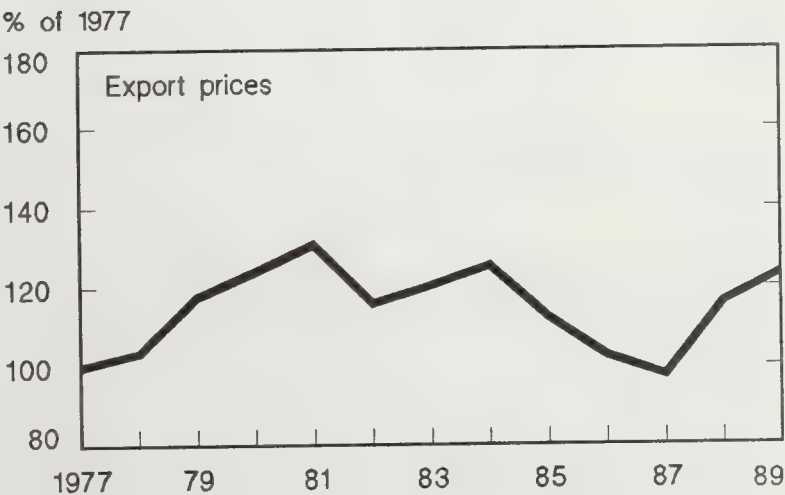
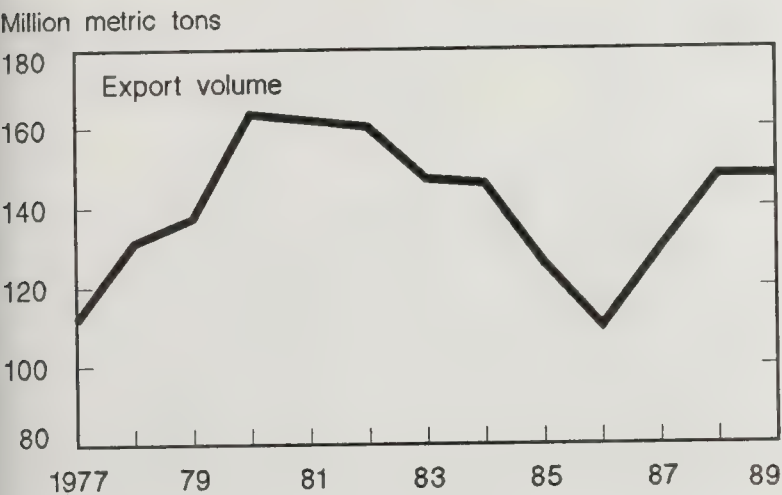


Capital formation is the repair and maintenance of existing income-earning real assets (such as housing, manufacturing plants, and so on) and the creation of new income-earning goods and services.

U.S. Trade

Export volume remained unchanged. Substantial declines in soybeans (down 7 million tons), wheat (down 2.8 million tons), and soybean meal (down 1.5 million tons) offset increases in corn (6.8 million tons) and sorghum (2 million tons). Export prices increased 6 percent. The real exchange rate index increased for all commodities in 1989, putting downward pressure on exports.

Chart 177
U.S. agricultural trade indicators



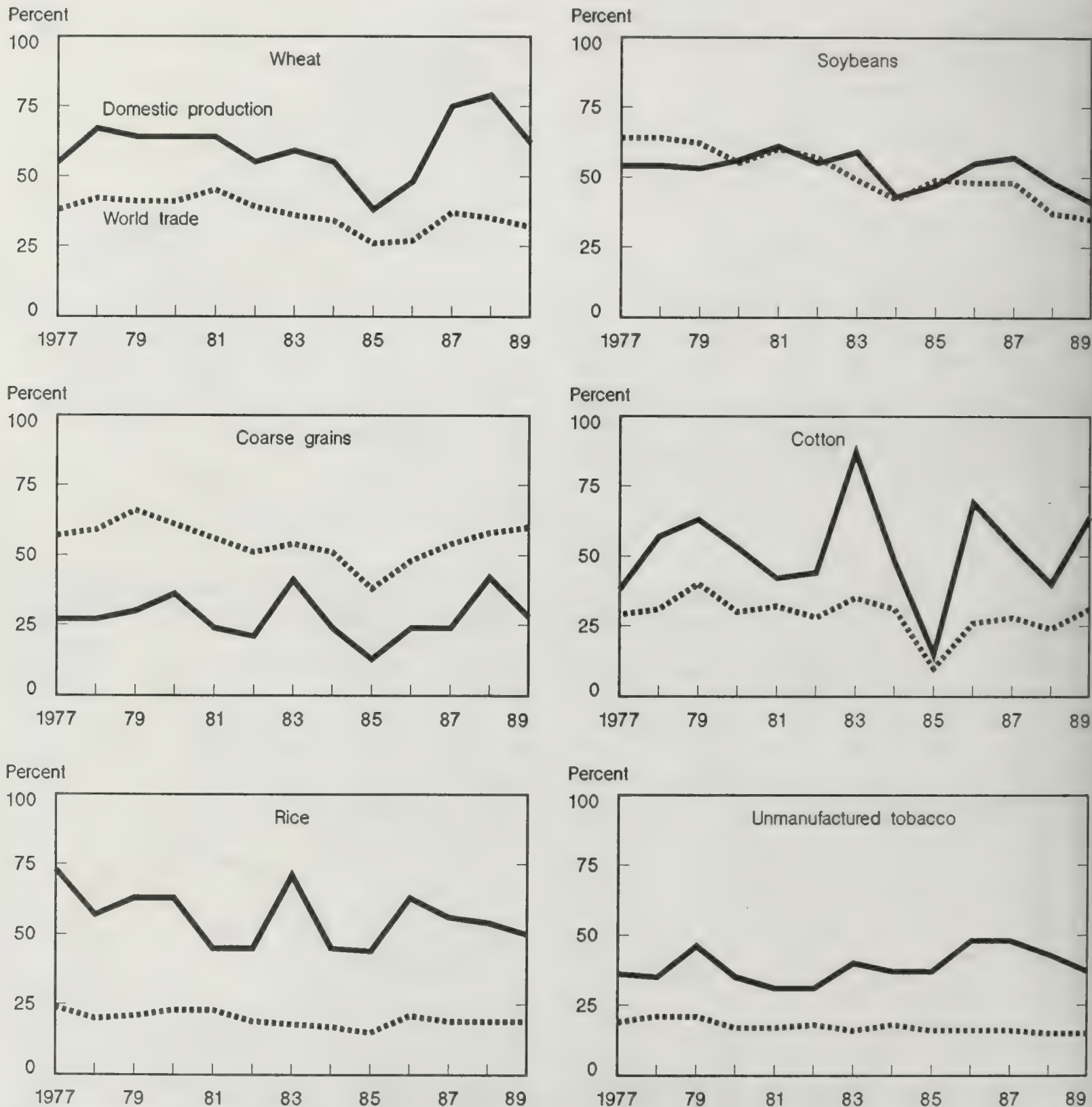
Foreign currency value of the U.S. dollar, weighted by relative size of agricultural trade with the United States, adjusted for inflation by use of a Consumer Price Index for the countries involved. An increasing value indicates that the dollar appreciated against the basket of currencies represented in that commodity market.

U.S. Trade

Exports of 1989/90 wheat took 62 percent of the total U.S. crop, down from over 75 percent of the 1988/89 crop. The export share of soybeans is expected to fall to its lowest level in over 20 years. U.S. share of the world market for both crops has likewise declined.

Chart 178

U.S. exports: Share of domestic production and world trade



Crop years used for share of domestic production.

U.S. Trade

Average farm prices were at a record level in 1989. Wheat, corn, and soybean export prices experienced a second consecutive year of significant increases. Farm export values in 1989 were at their highest level since the 1981 record.

Chart 179

U.S. agricultural exports and farm prices

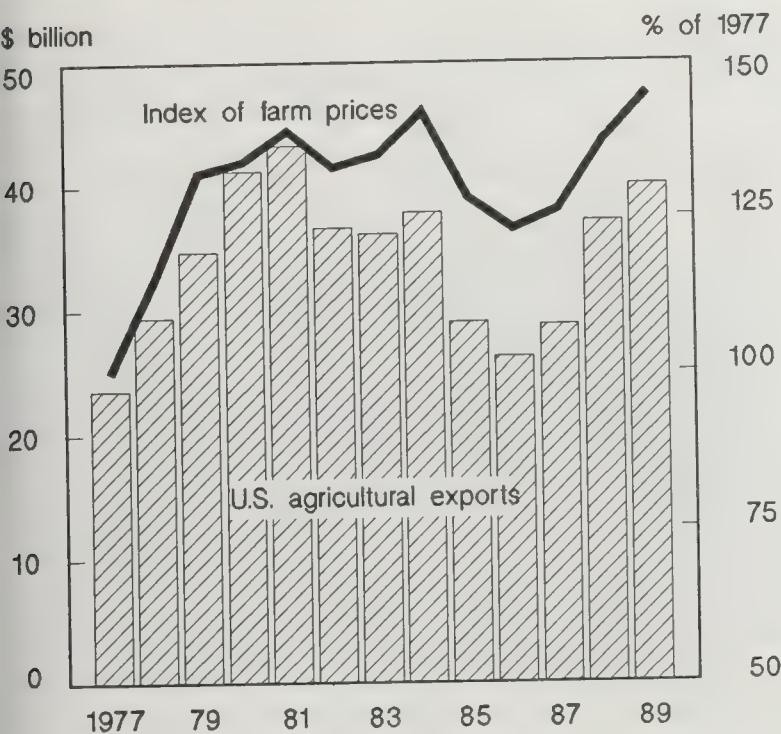


Chart 180

Export prices for major U.S. crops

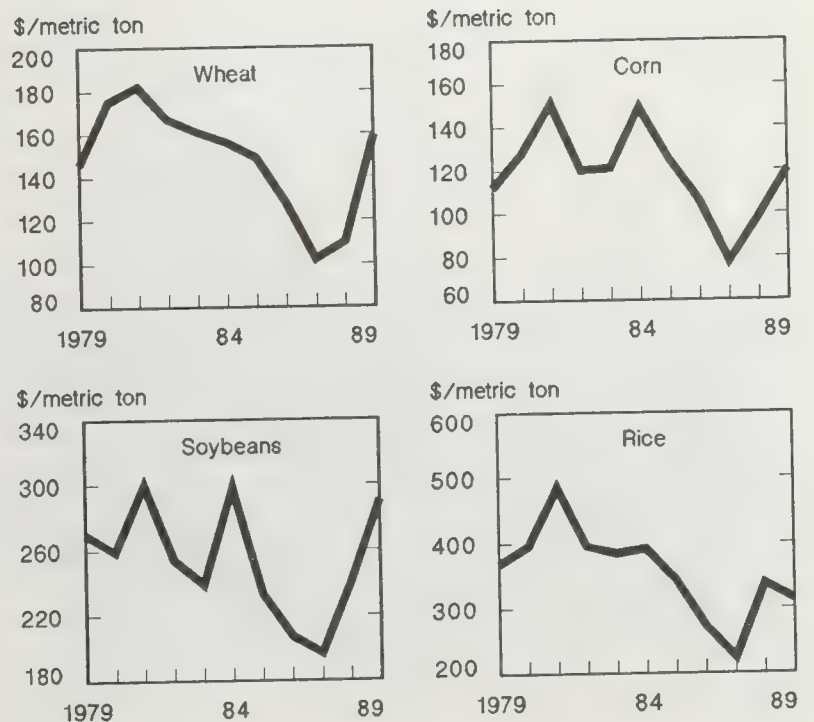


Chart 181

Value of U.S. agricultural exports by commodity

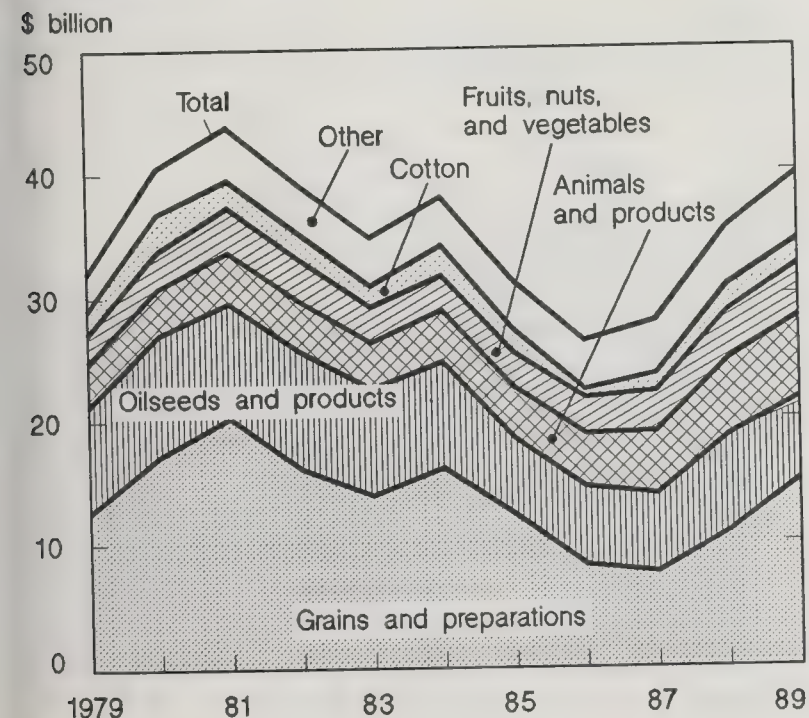
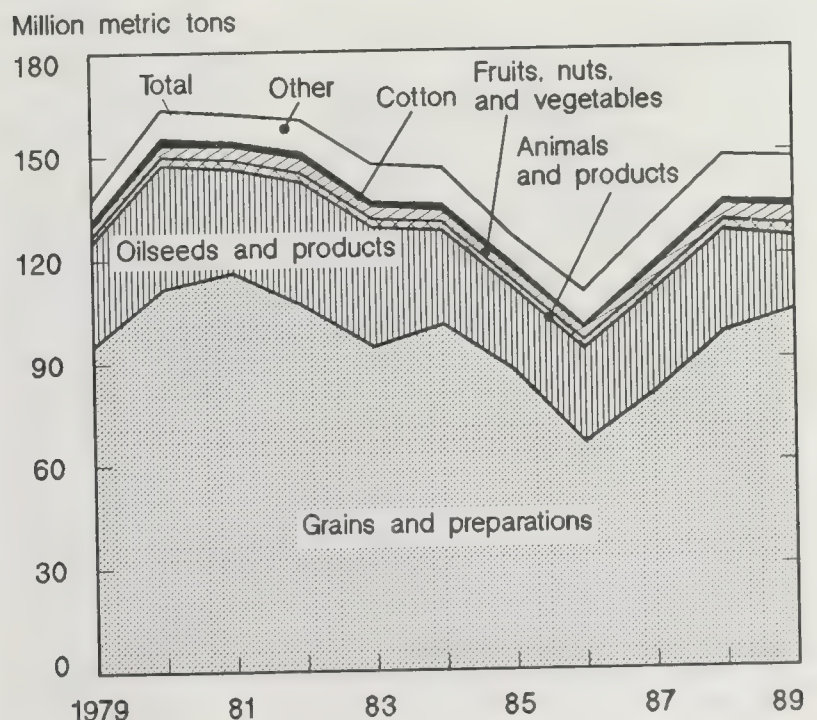


Chart 182

Volume of U.S. agricultural exports by commodity



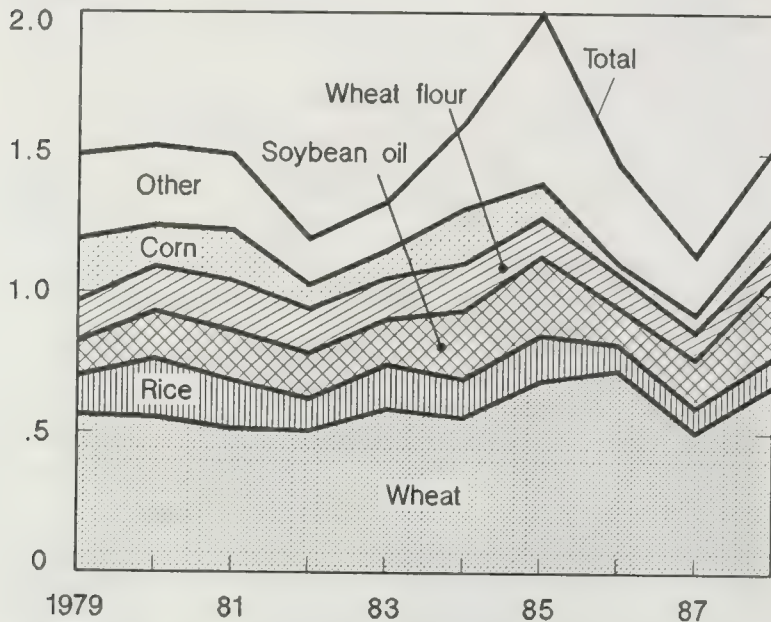
U.S. Trade

Concessional sales jumped by a third to \$1.5 billion. Wheat, rice, and soybean oil accounted for 70 percent of total sales. U.S. agricultural exports to Asia jumped to a high of \$18.7 billion. Exports of a record \$2.8 billion to Mexico boosted sales to Latin America to \$5.4 billion, its highest level since 1981.

Chart 183

Concessional export sales of U.S. agricultural products

\$ billion



Other includes corn-soya-milk blend, nonfat dry milk, cornmeal, oilcake and meal, cotton, and tobacco.

Chart 184

U.S. agricultural exports to Asia

\$ billion

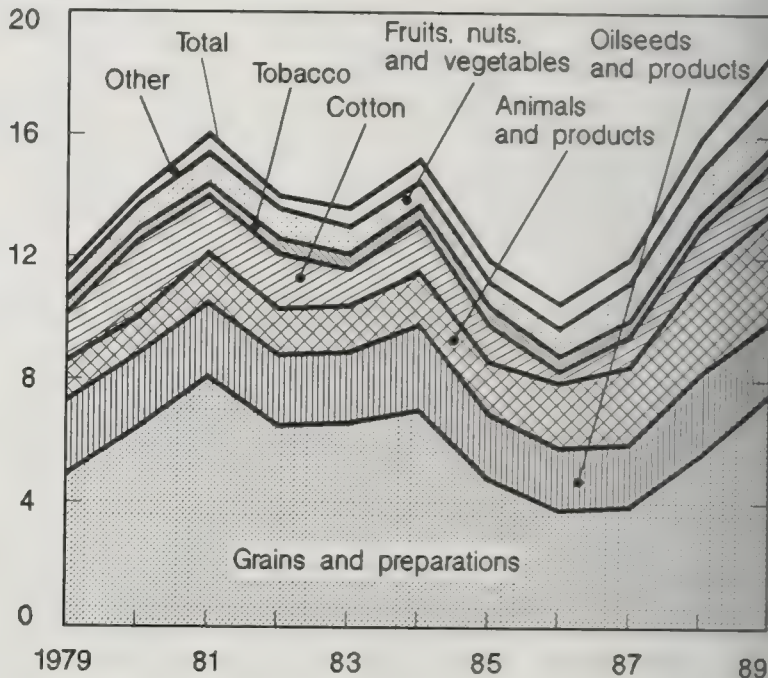


Chart 185

U.S. agricultural exports to Africa

\$ billion

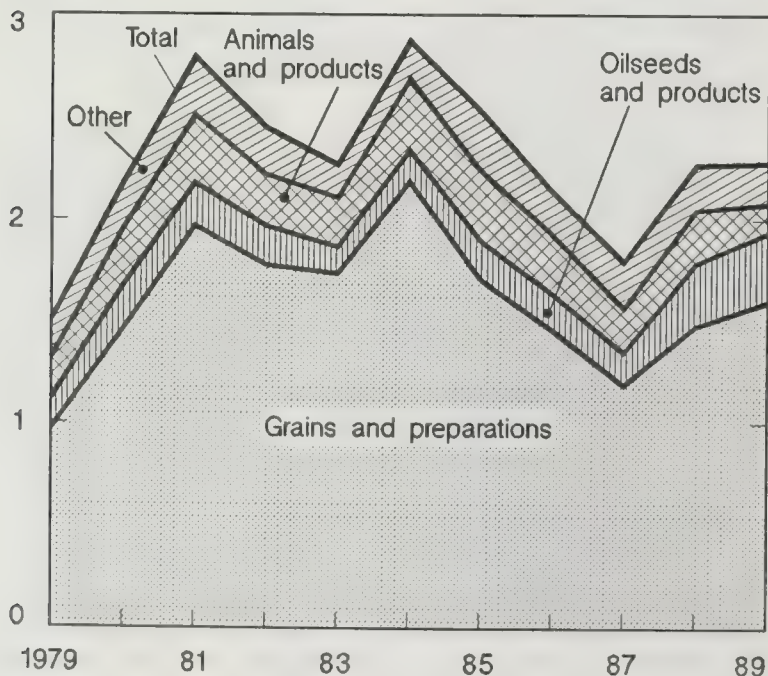
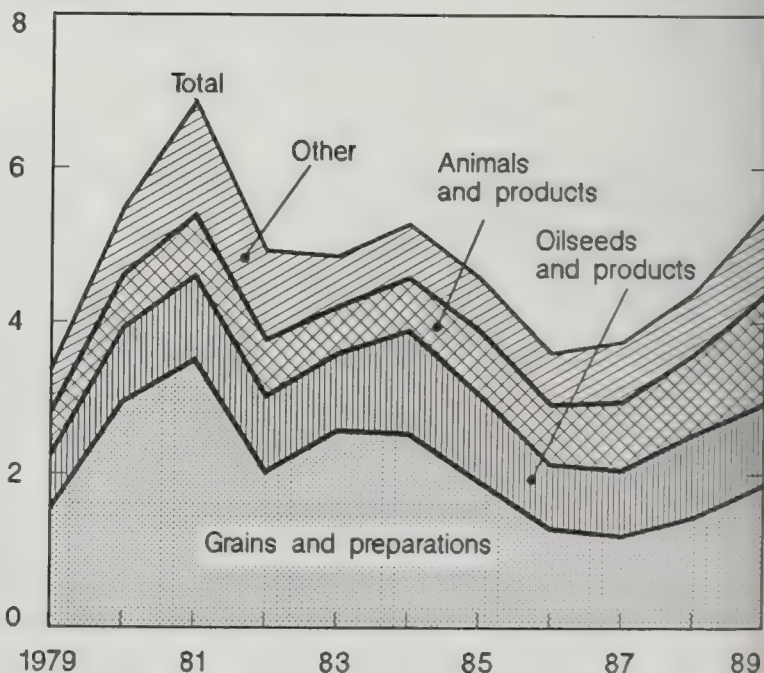


Chart 186

U.S. agricultural exports to Latin America

\$ billion



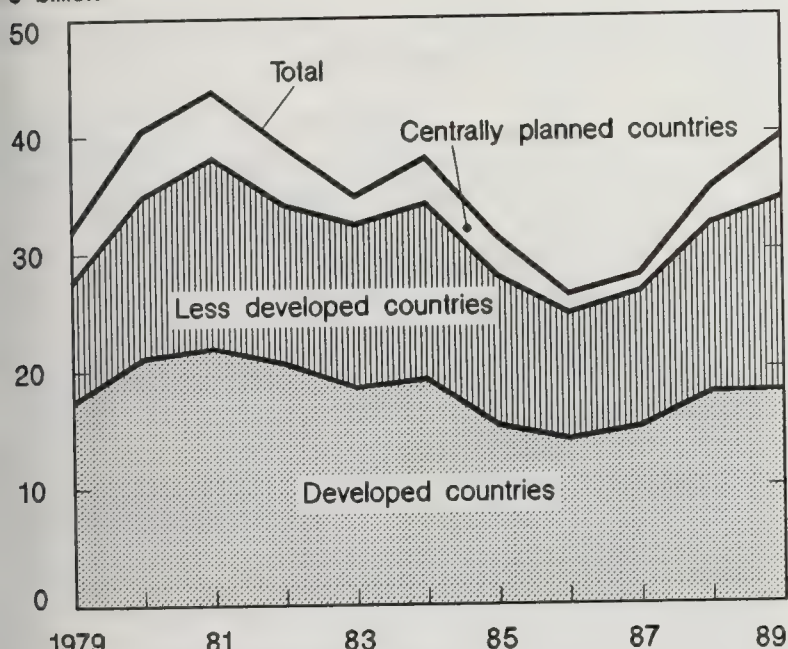
U.S. Trade

Exports to centrally planned countries increased 71 percent from 1988. The Soviet Union and China were the two largest markets. A record \$3 billion of animal product exports went to less developed countries (LDC's) in 1989, pushing total U.S. exports to these countries to a new high of \$16.4 billion.

Chart 187

U.S. agricultural exports to major areas

\$ billion



Adjusted for transshipments through Canada.

Chart 188

U.S. agricultural exports to centrally planned countries

\$ billion

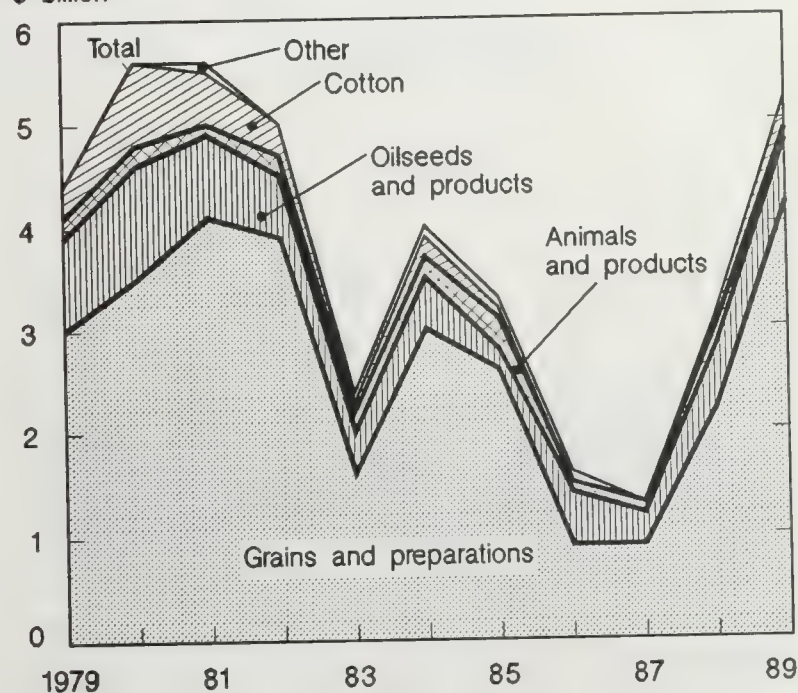


Chart 189

U.S. agricultural exports to less developed countries

\$ billion

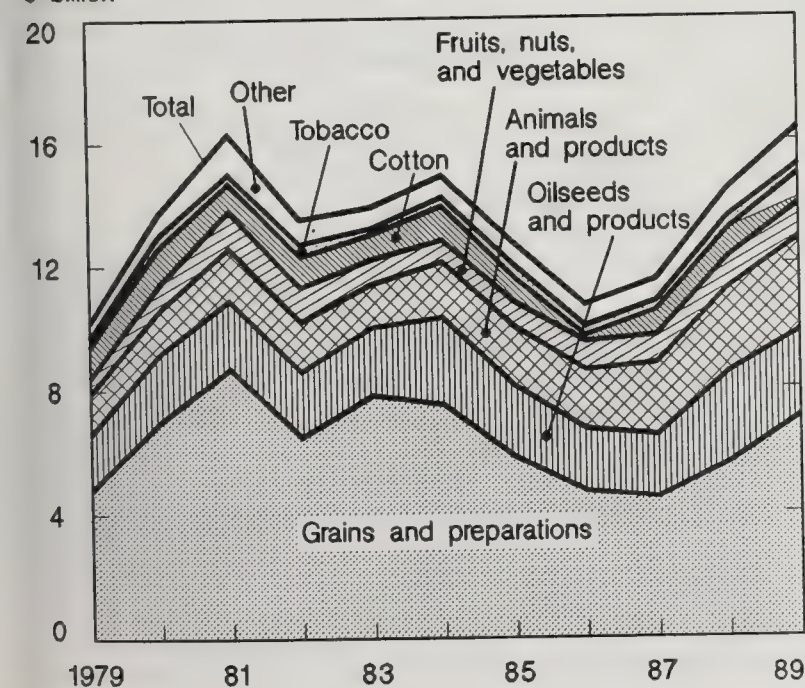
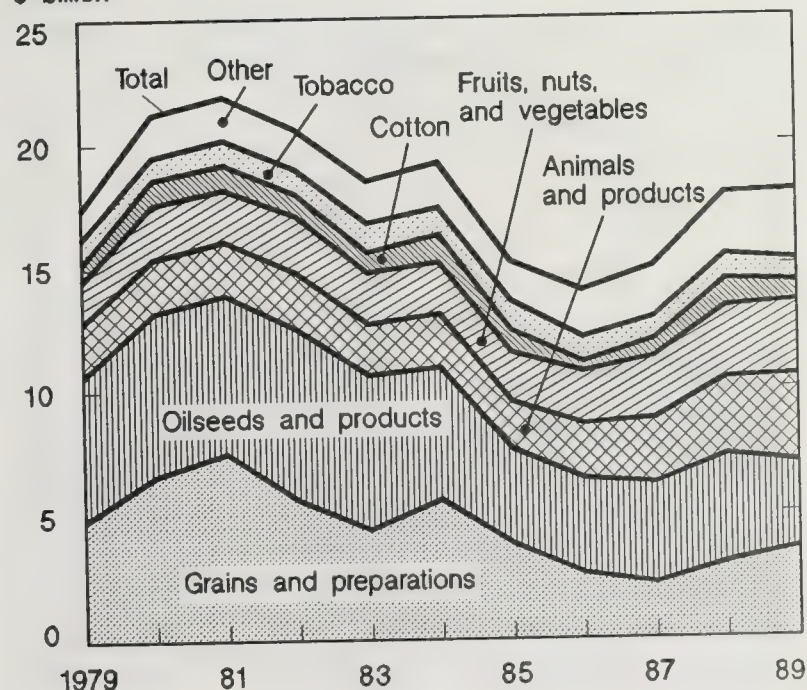


Chart 190

U.S. agricultural exports to developed countries

\$ billion

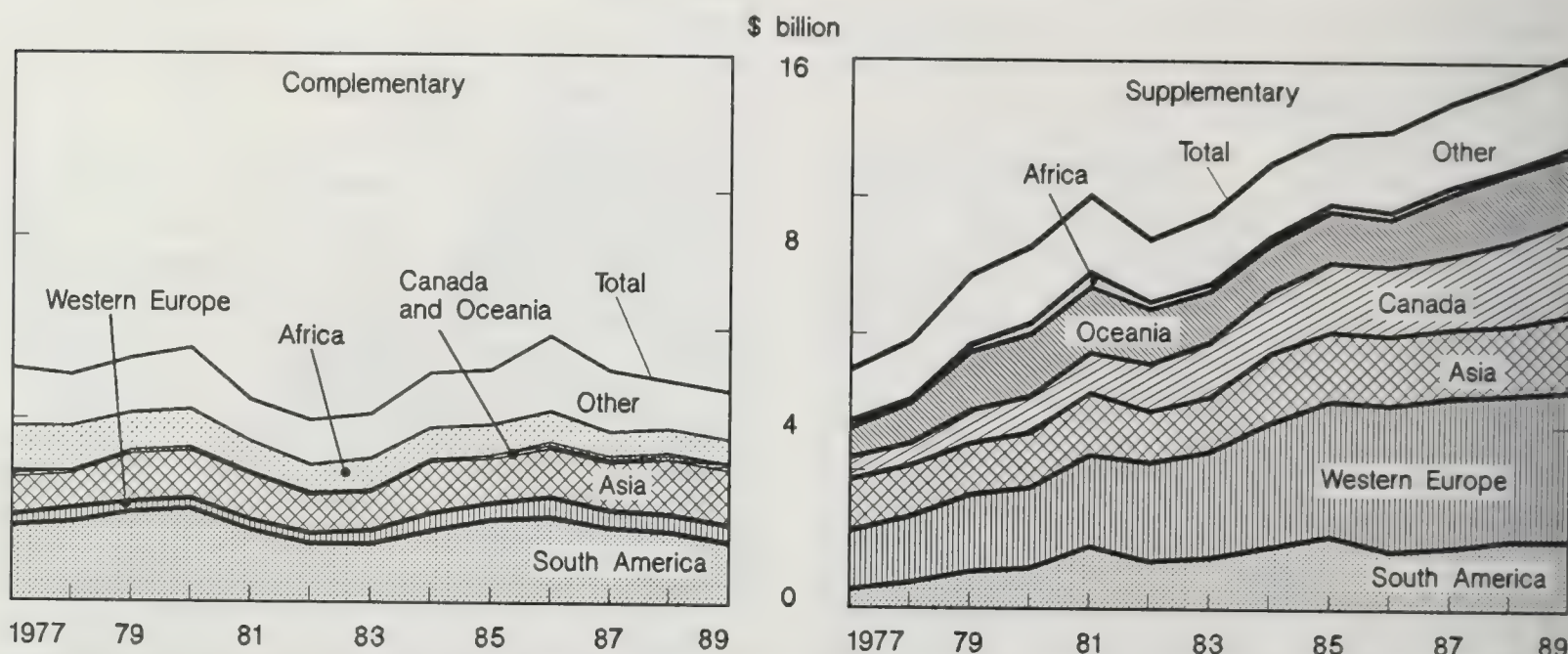


U.S. Trade

Asia is gaining on South America as the largest supplier of noncompetitive (complementary) products to the United States. Noncompetitive imports fell for the third straight year in 1989, mostly due to the decline in the value of coffee and cocoa imports. Competitive (supplementary) imports rose for the seventh consecutive year as a result of record fruit, vegetable, and other imports.

Chart 191

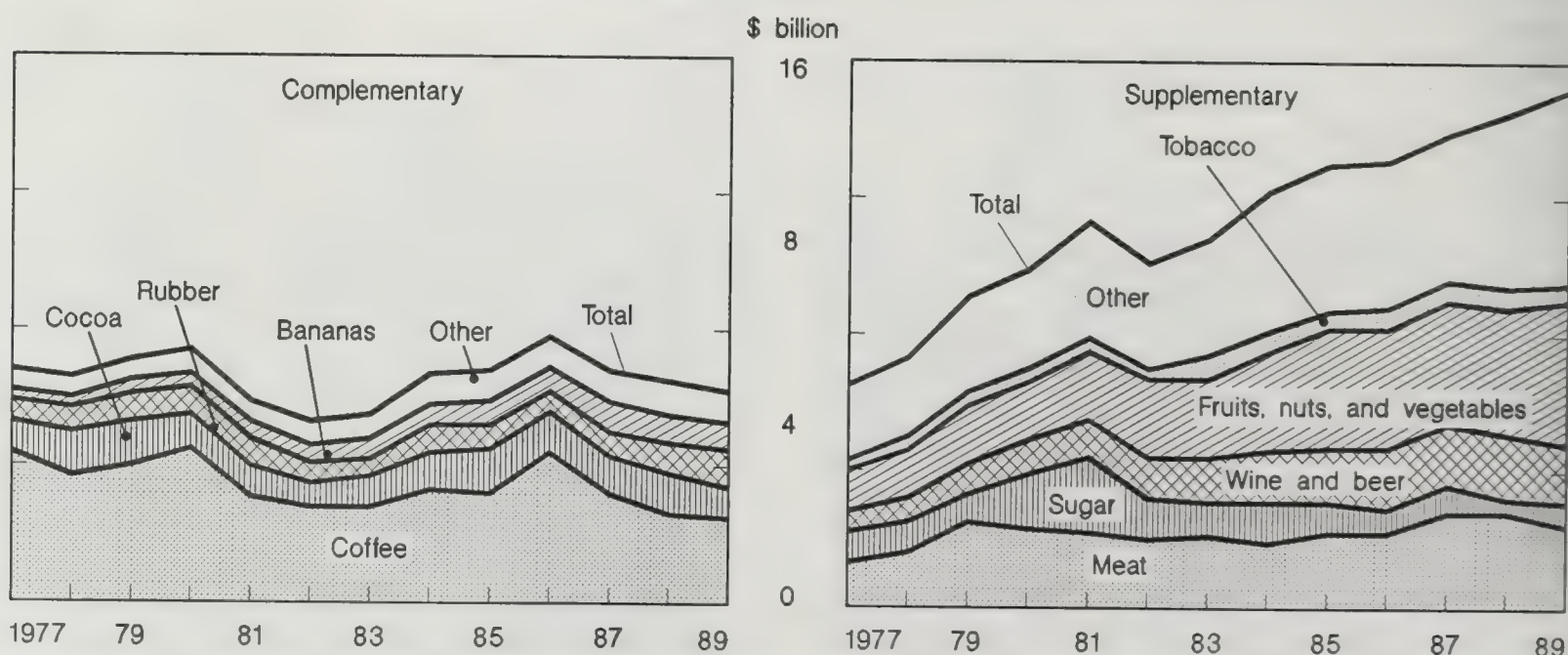
Origin of U.S. agricultural imports



Complementary imports are those which do not compete with U.S. agricultural products, such as coffee, cocoa, and bananas. Supplementary imports compete with domestically produced products such as meat and sugar. Other includes Eastern Europe, Soviet Union, Mexico, Central America, and the Caribbean.

Chart 192

U.S. agricultural imports by commodity



Complementary imports are those which do not compete with U.S. agricultural products, such as coffee, cocoa, and bananas. Supplementary imports compete with domestically produced products such as meat and sugar.

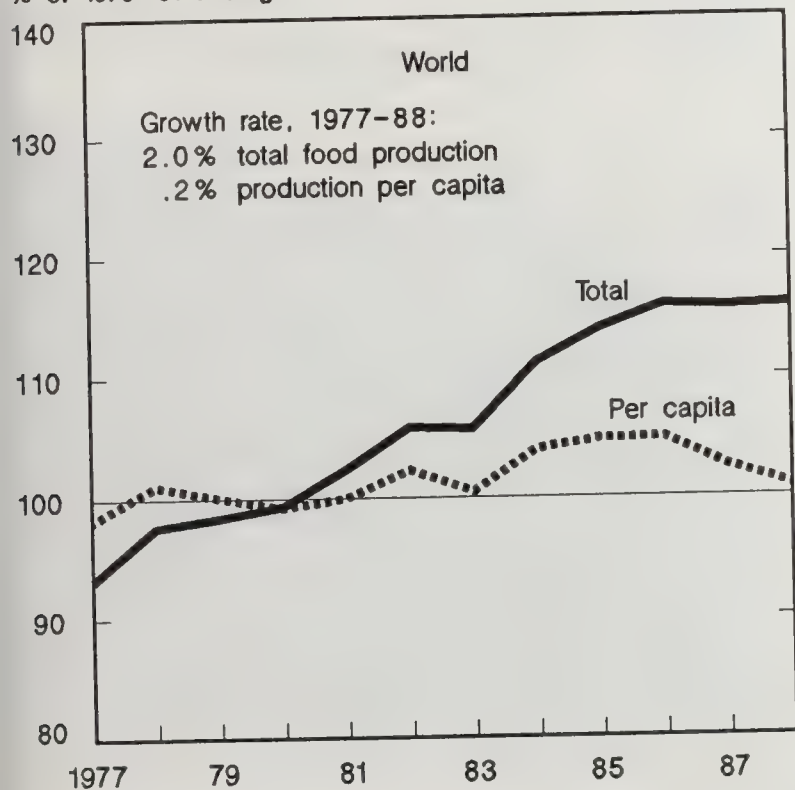
World Production

World food production was unchanged in 1988. Production in developed markets fell by 4 percent, led by the drought-induced decline in the United States. Less developed countries increased production by 5 percent. With the exception of centrally planned countries, growth in per capita food production was perilously low in the last decade.

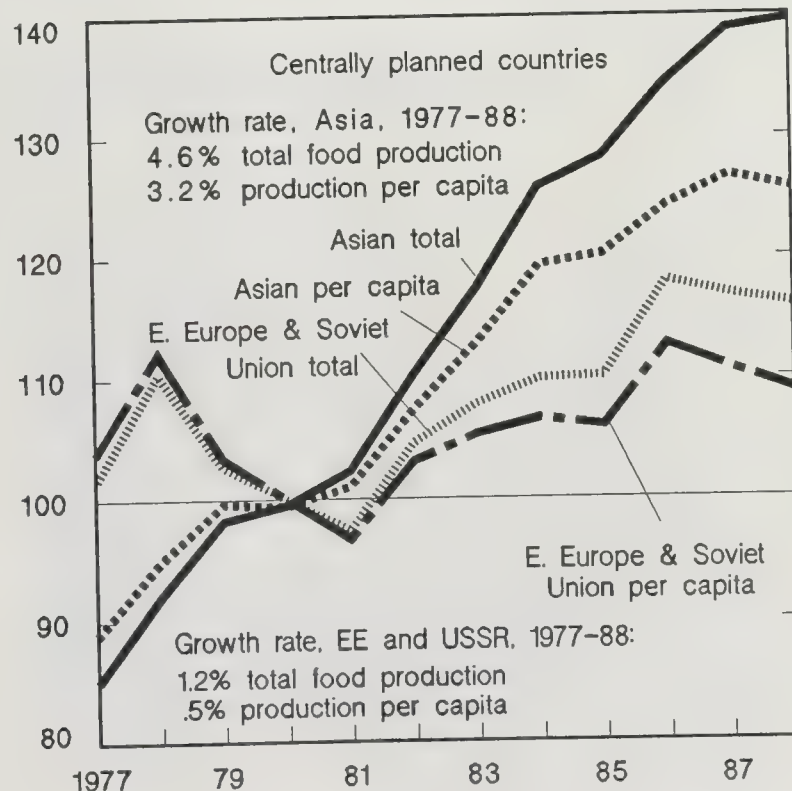
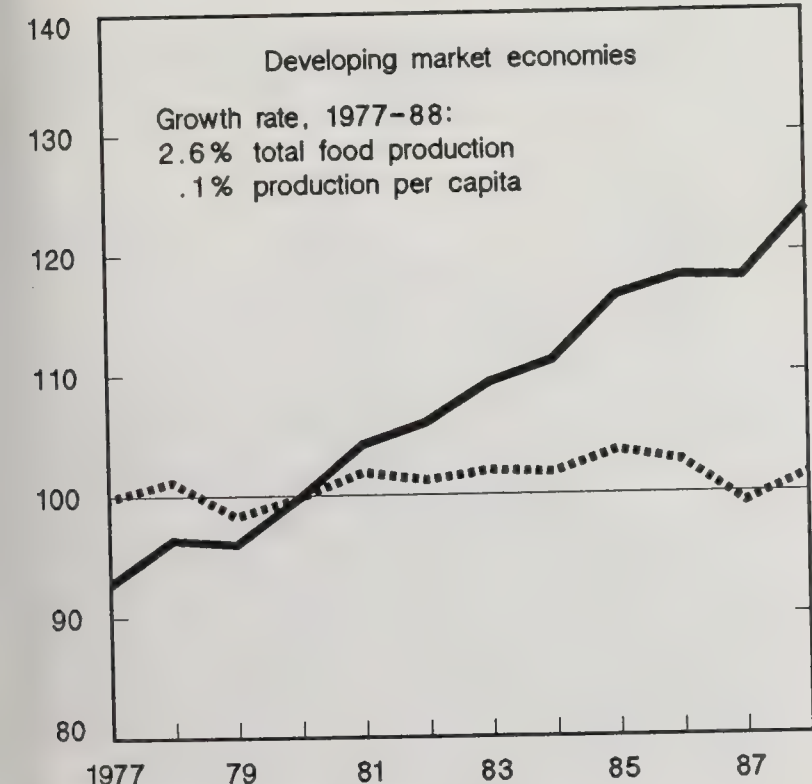
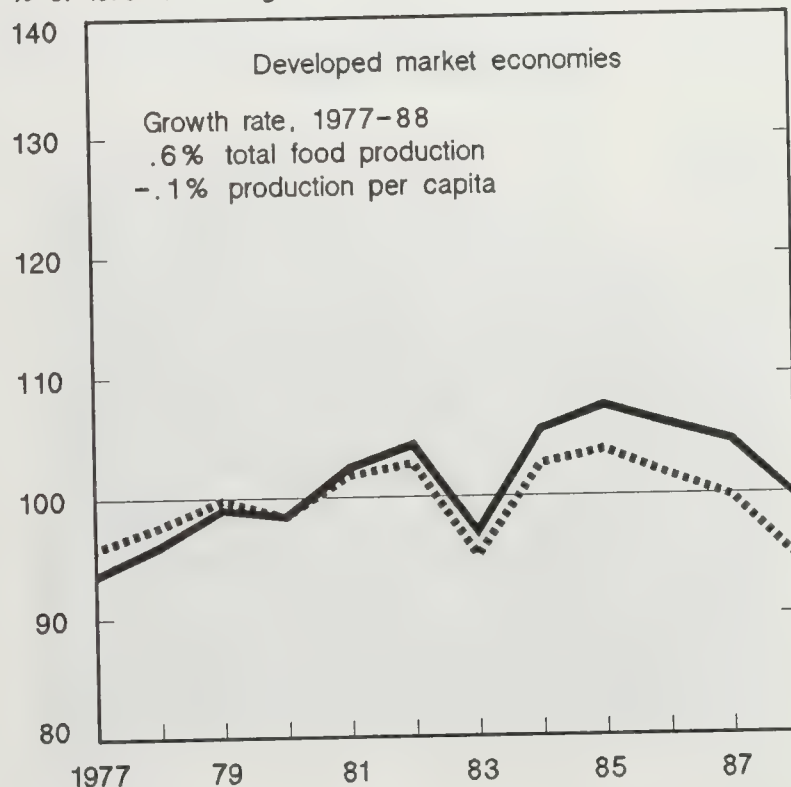
Chart 193

Changes in world food production

% of 1979-81 average



% of 1979-81 average



Compound annual growth rates computed for 1977-88.

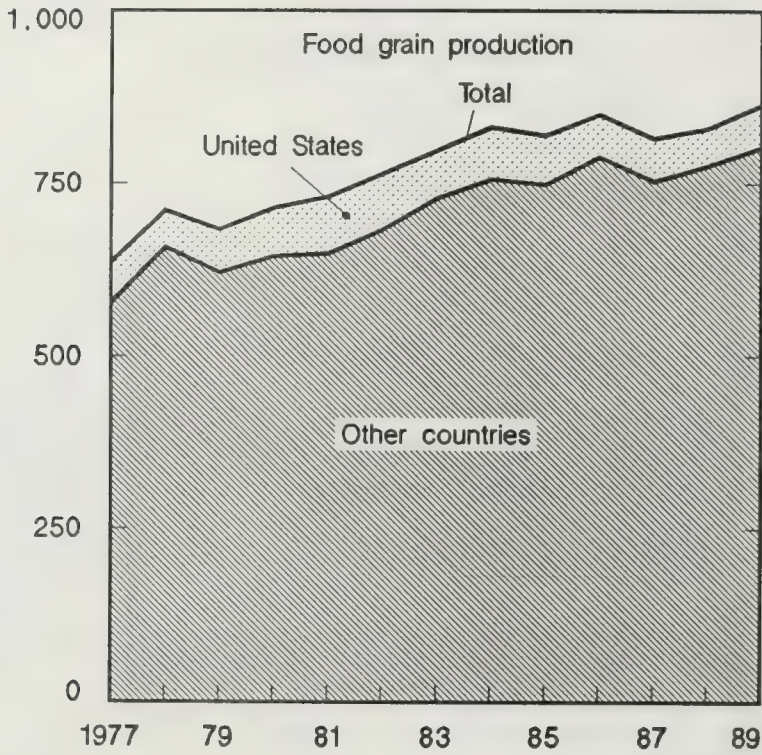
World Production

The 1989 world food grain crop is projected to be a record 863 million tons. China, the Soviet Union, the EC, India, Canada, Argentina, and the United States increased wheat production by 39 million tons. Nonetheless, utilization is expected to exceed output. Both carryover stocks and exports continue to fall.

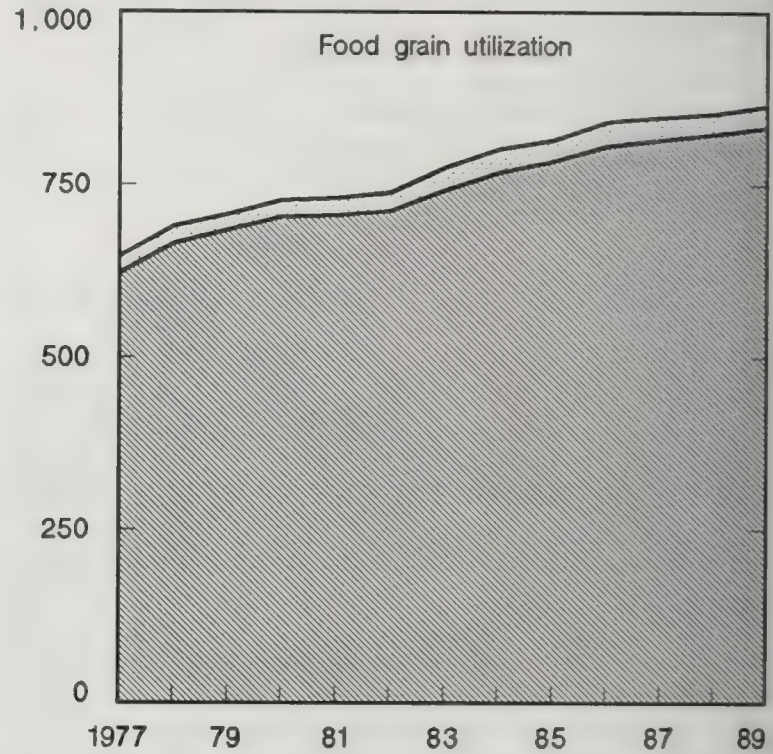
Chart 194

World and U.S. food grain production, utilization, carryover, and exports

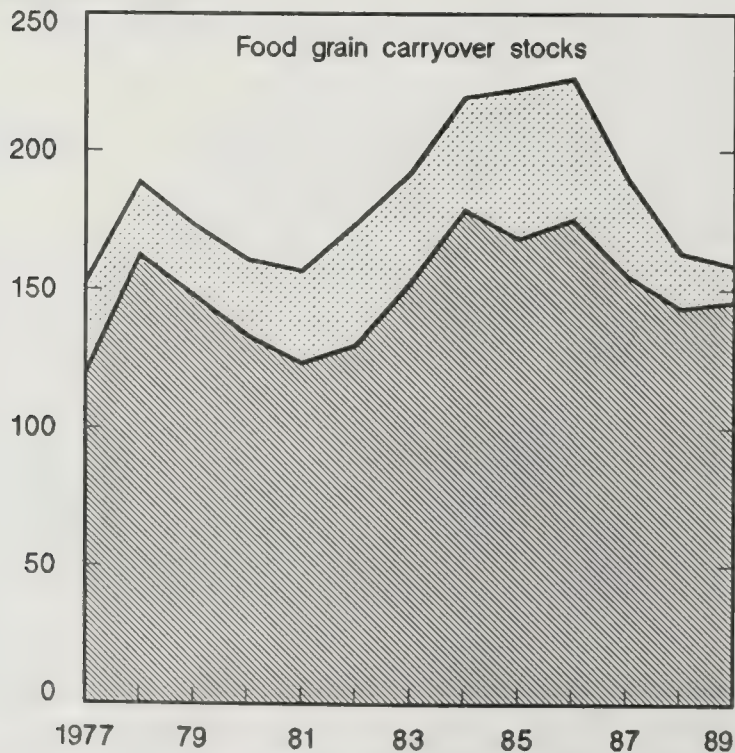
Million metric tons



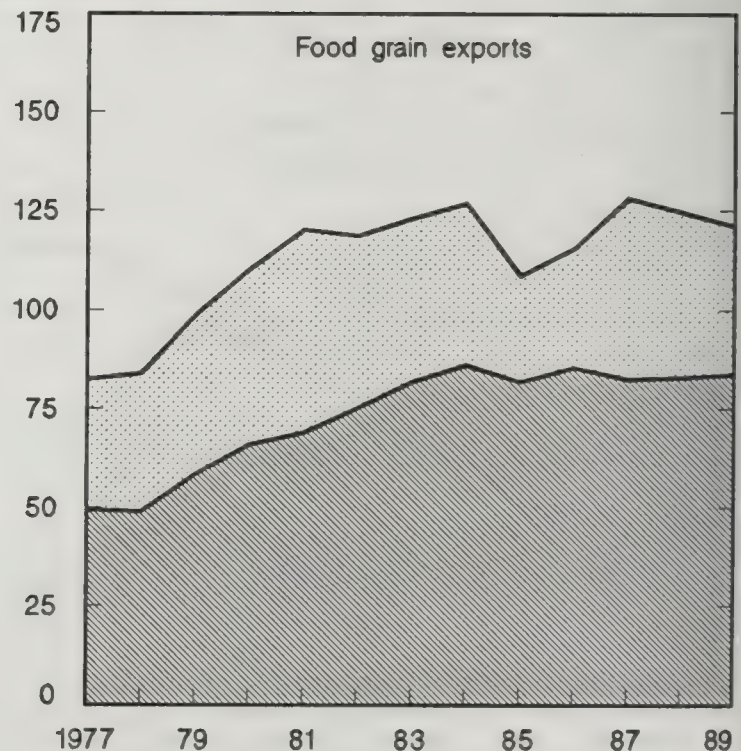
Million metric tons



Million metric tons



Million metric tons



Food grains include wheat and milled rice.

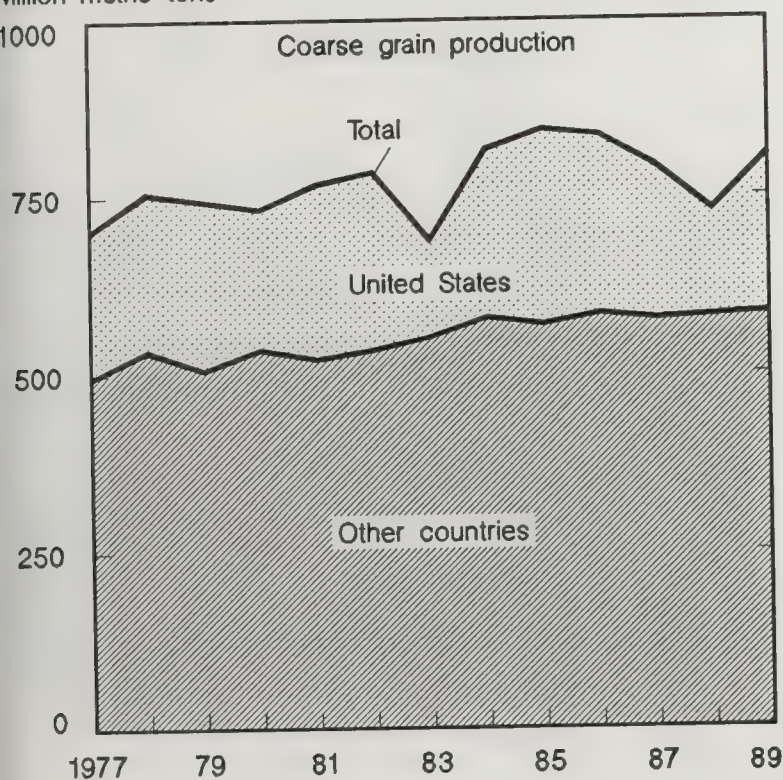
World Production

Global coarse grain production increased by 11 percent. Utilization is expected to exceed output for a third consecutive year. This should draw down stocks by 8 percent or 12 million tons. The U.S. share of world exports of coarse grains is expected to rise slightly in 1989 over its 58-percent share in 1988.

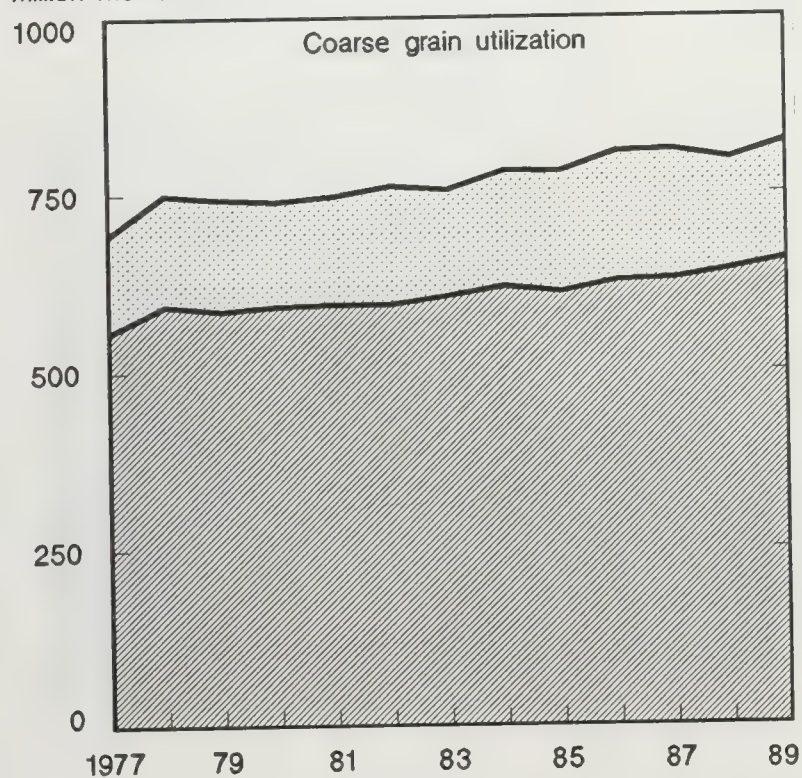
Chart 195

World and U.S. coarse grain production, utilization, carryover, and exports

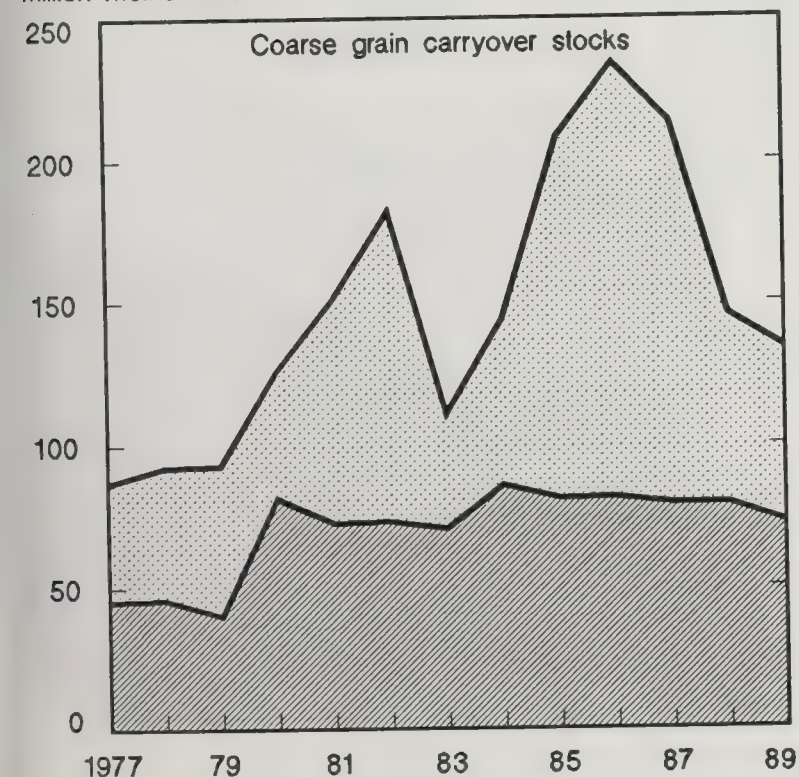
Million metric tons



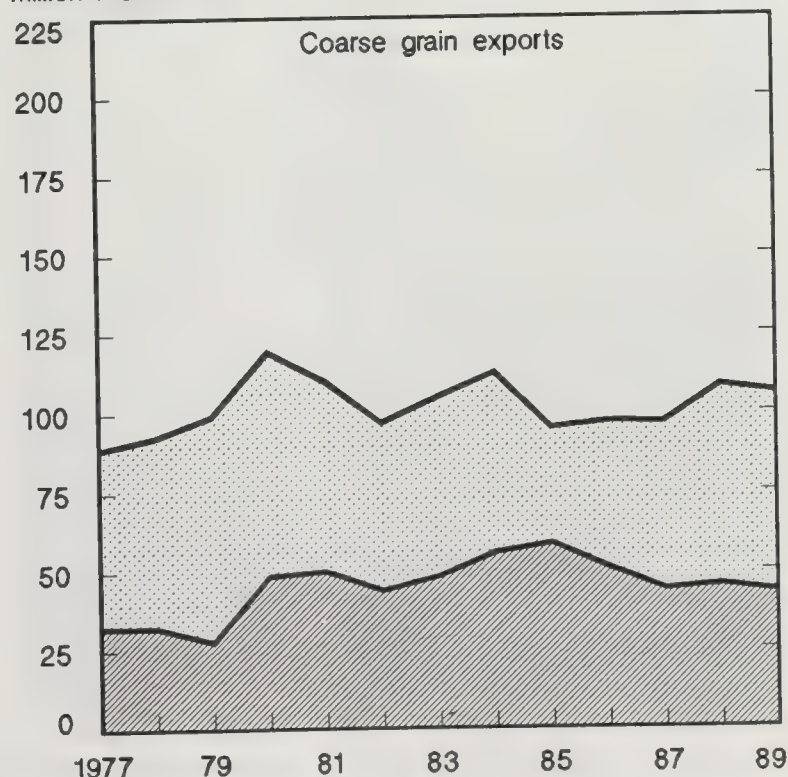
Million metric tons



Million metric tons



Million metric tons



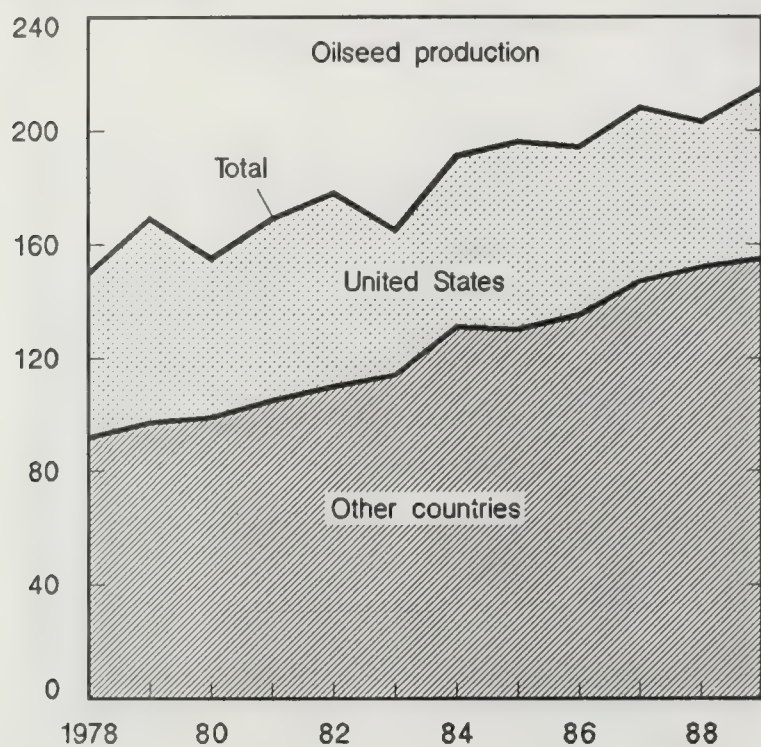
World Production

World oilseed production has averaged 3.3 percent growth per year since 1978, compared with 1.8 and 0.6 percent growth for food grains and feed grains. Exports play a larger role in oilseeds than in grains.

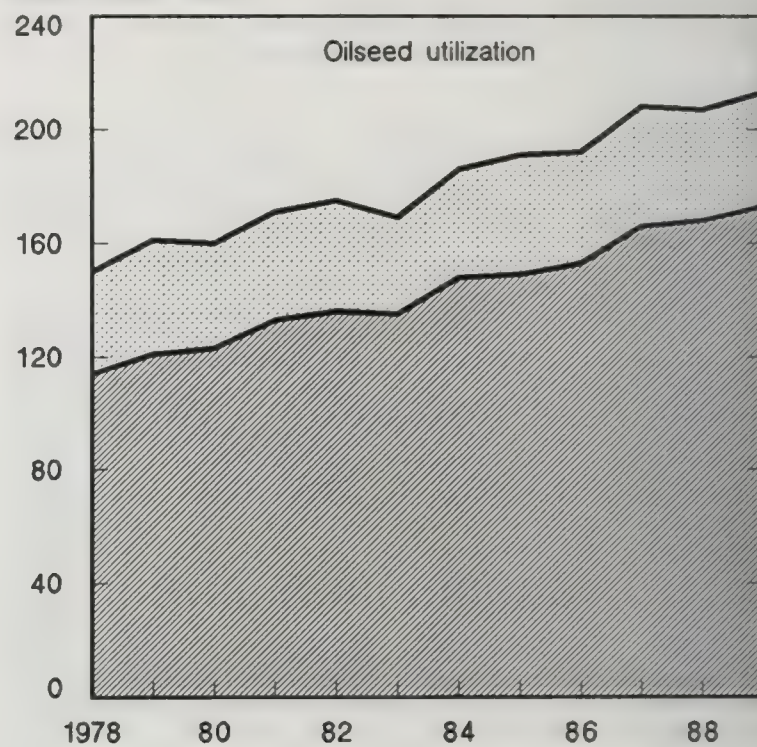
Chart 196

World and U.S. oilseed production, utilization, carryover, and exports

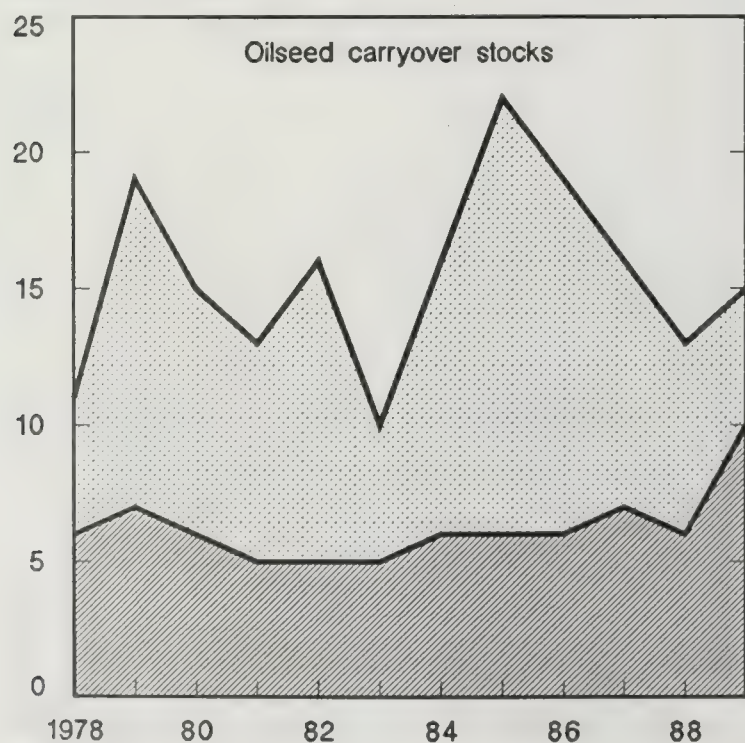
Million metric tons



Million metric tons



Million metric tons



Million metric tons



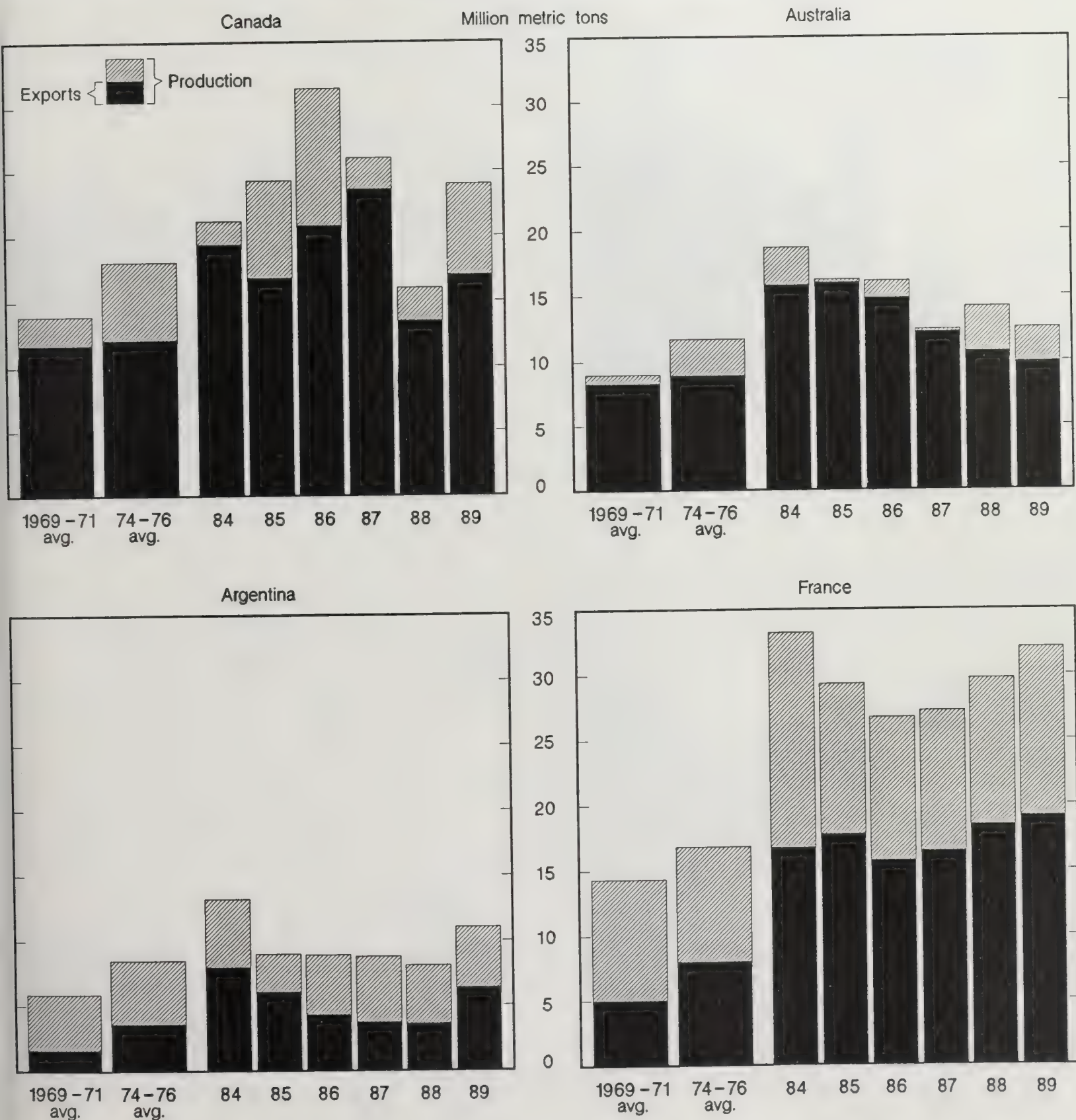
Oilseeds include soybeans, cottonseed, sunflowers, peanuts, rapeseed, flaxseed, palm kernel, and copra.

World Trade

Canadian wheat production recovered to 24 million tons. Wheat output in Argentina increased to 11 million tons after 4 years under 9 million tons. Australian wheat production continued low at 12.5 million tons and exports are expected to fall.

Chart 197

Wheat export competitors: Canada, Australia, Argentina, and France

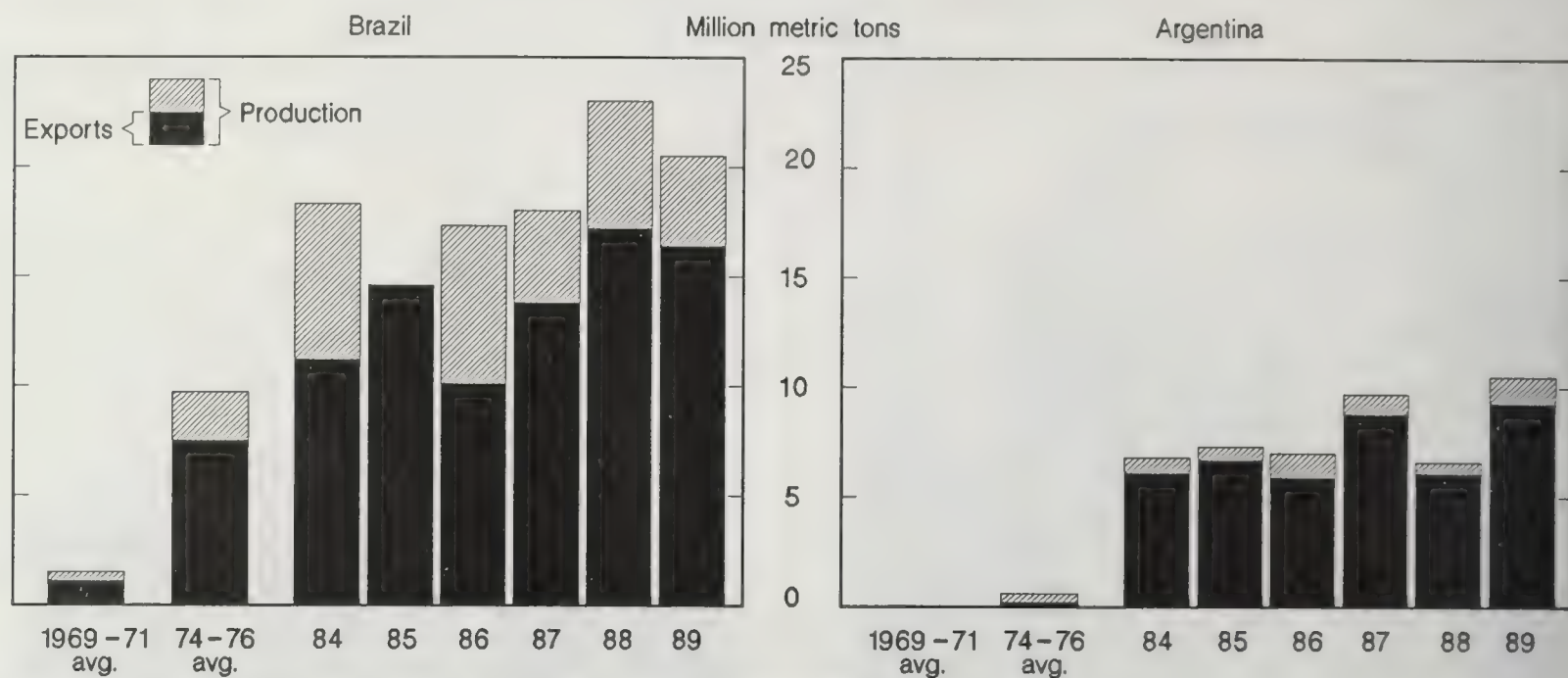


World Trade

Argentine soybean production and exports are projected to reach record levels. Brazilian soybean production remained high. Thailand is forecasting a record rice crop in 1989 of 14.2 million tons. Thai rice exports are now double those of the United States.

Chart 198

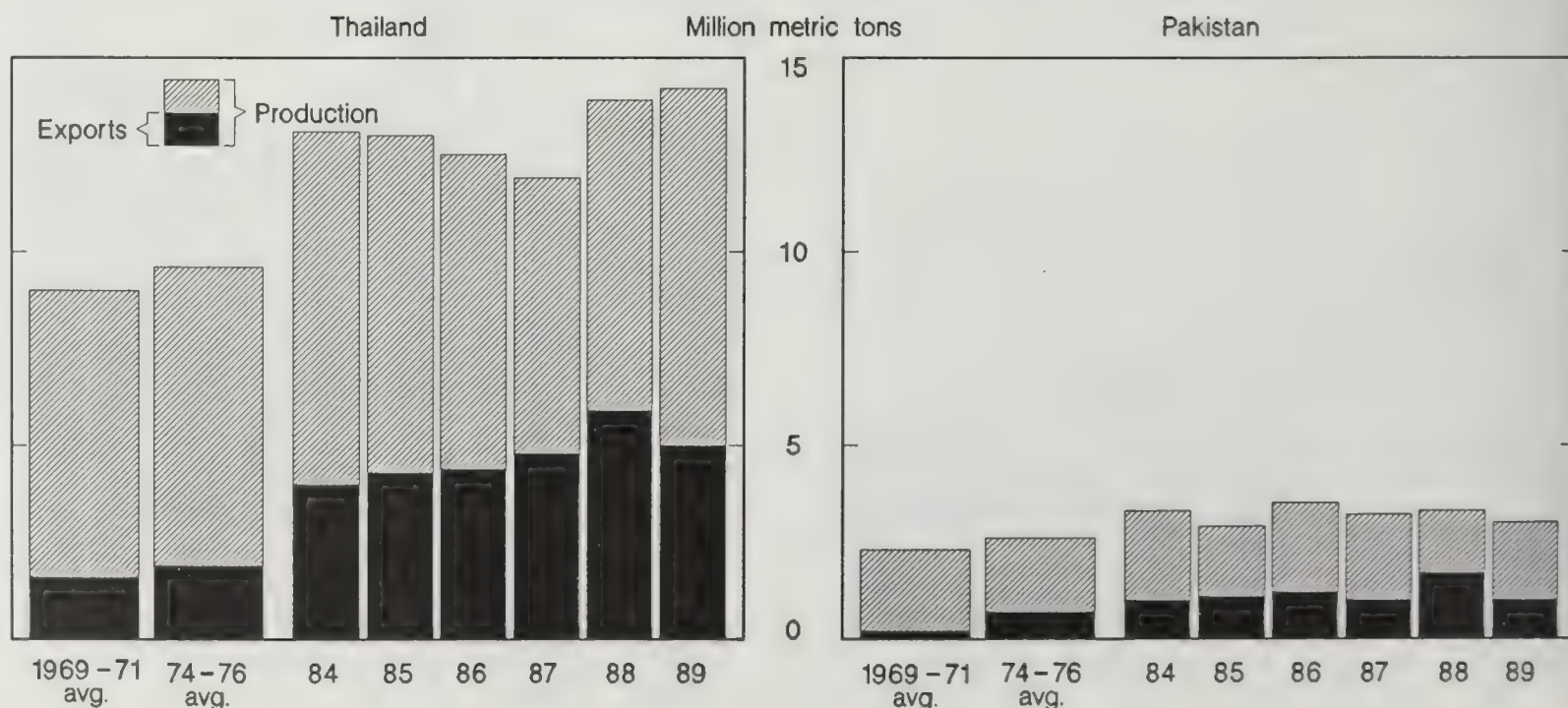
Soybean export competitors: Brazil and Argentina



Includes soybean meal and oil in bean equivalent. No commercial production for Argentina, 1969-71.

Chart 199

Rice export competitors: Thailand and Pakistan

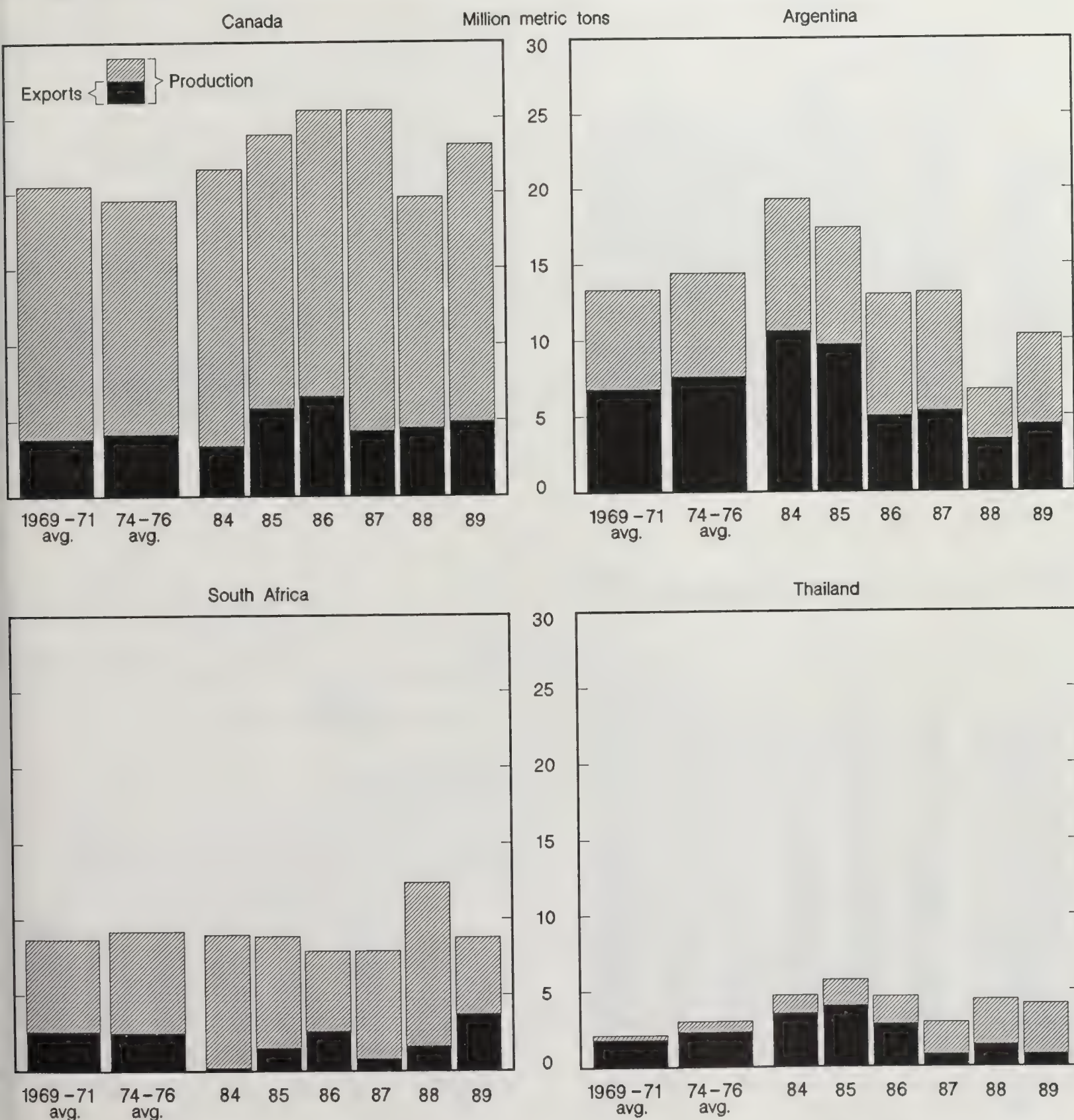


World Trade

Canada and Argentina rebounded from low coarse grain production in 1988. Only South Africa is expected to export near its capacity. Canada's barley exports and Argentina's corn and sorghum exports are forecast to rise, while Thai corn exports are expected to fall.

Chart 200

Coarse grain export competitors: Canada, Argentina, South Africa, and Thailand



World Trade

Soviet cotton production and exports have varied little since 1984. Pakistan's cotton production has climbed steadily and is forecast at 7.1 million tons in 1989. Nonetheless, exports are expected to decrease sharply from 1988's record 3.8 million tons. Both Brazil and Greece expect larger tobacco crops. Nearly all of the Greek crop is forecast to be exported.

Chart 201

Cotton export competitors: Soviet Union and Pakistan

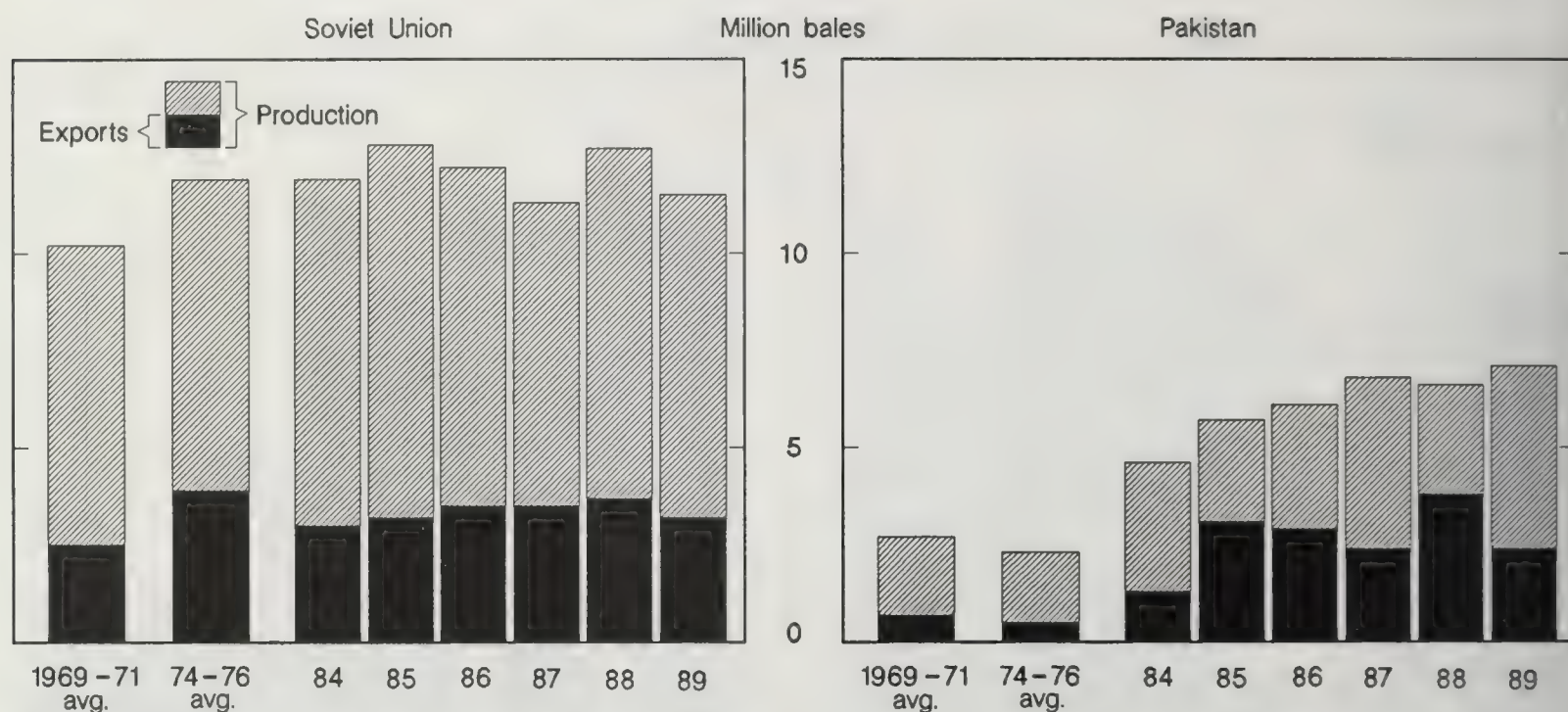
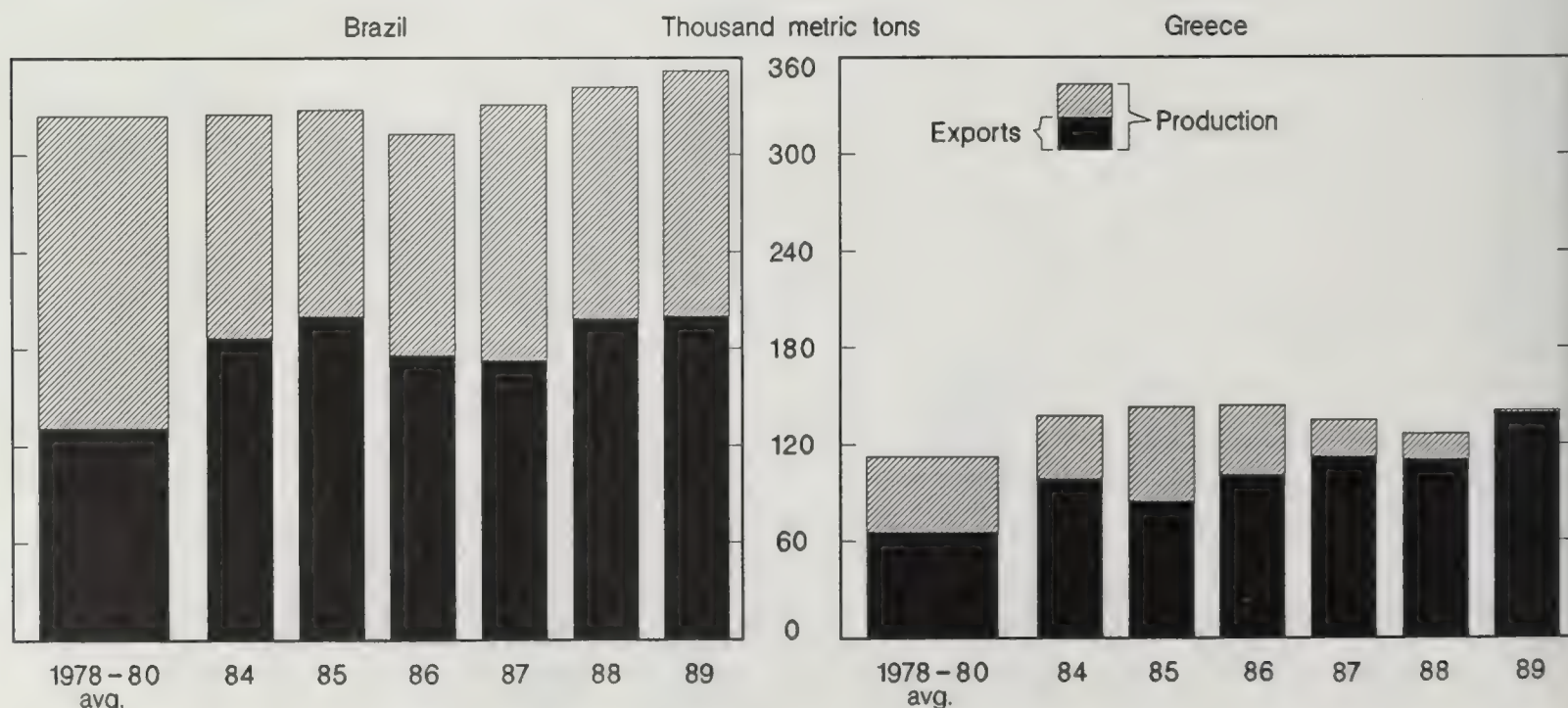


Chart 202

Tobacco export competitors: Brazil and Greece



Livestock

Total beef and veal exports are expected to fall due to declines in Australian and EC beef exports. U.S. exports of livestock products surpassed the 1988 high of \$5 billion. U.S. imports of red meats are expected to fall. Outlook for 1990 shows dairy cow numbers falling 1 percent and beef cow numbers rising 1-2 percent.

Chart 203
Beef and veal exports in major trading countries

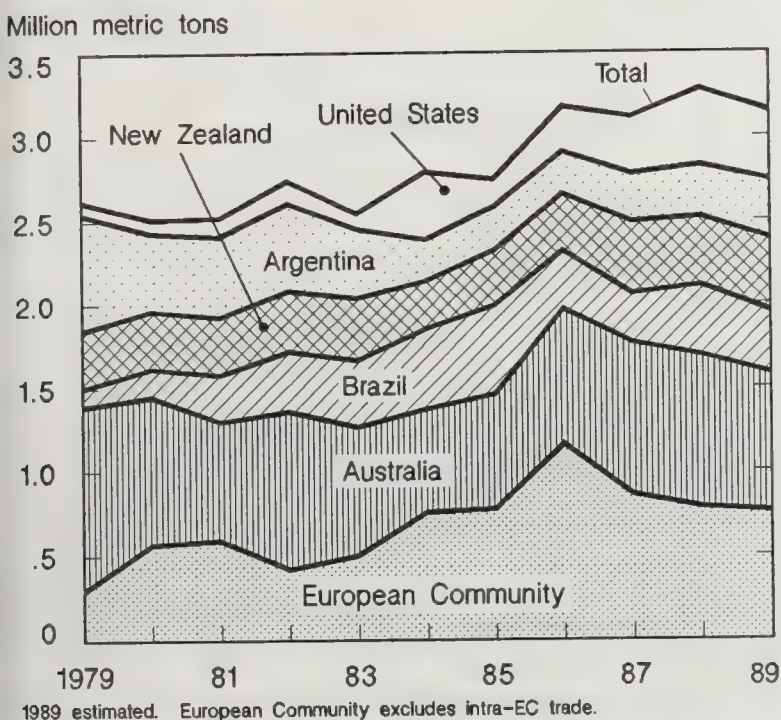


Chart 204
U.S. exports of livestock products

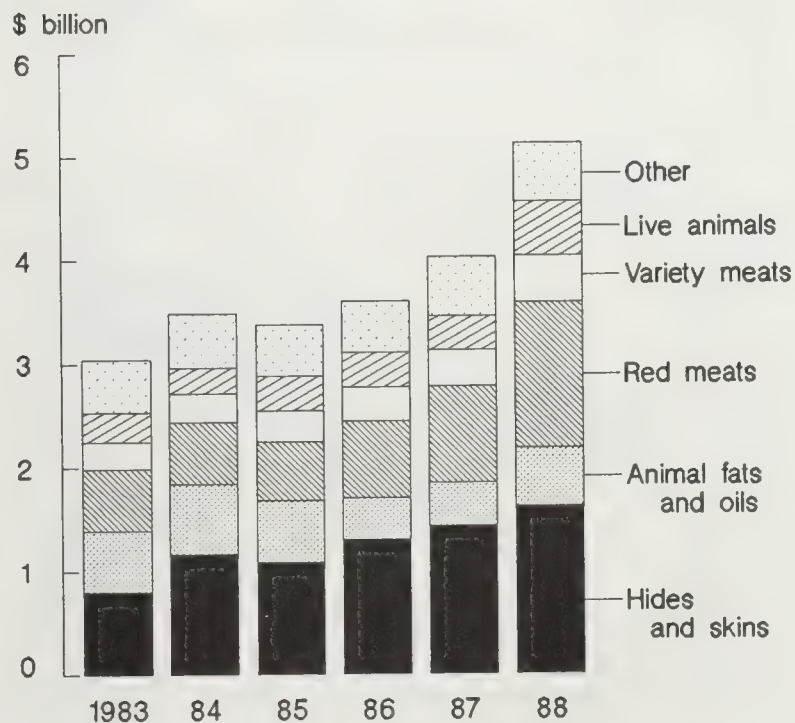


Chart 205
U.S. Imports of red meat

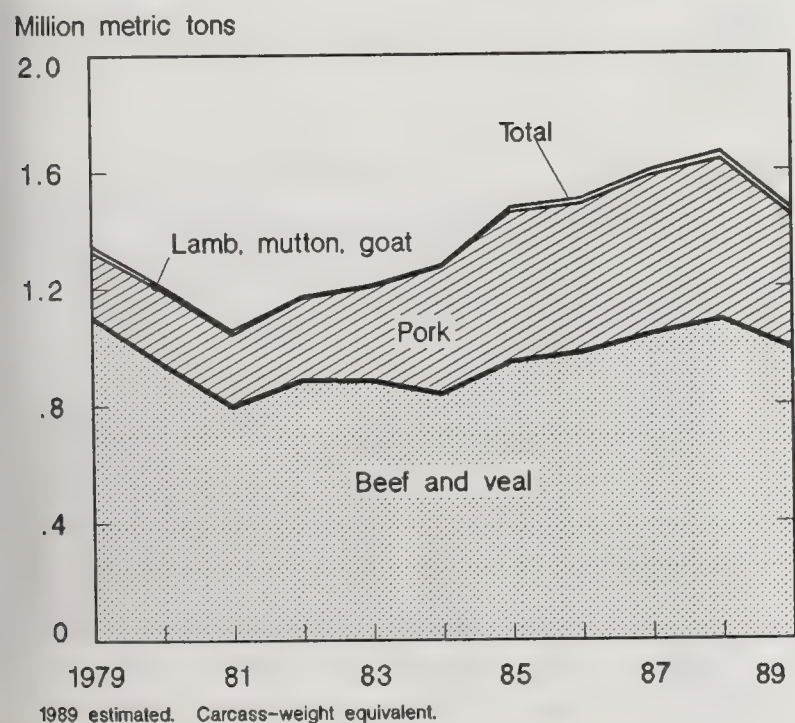
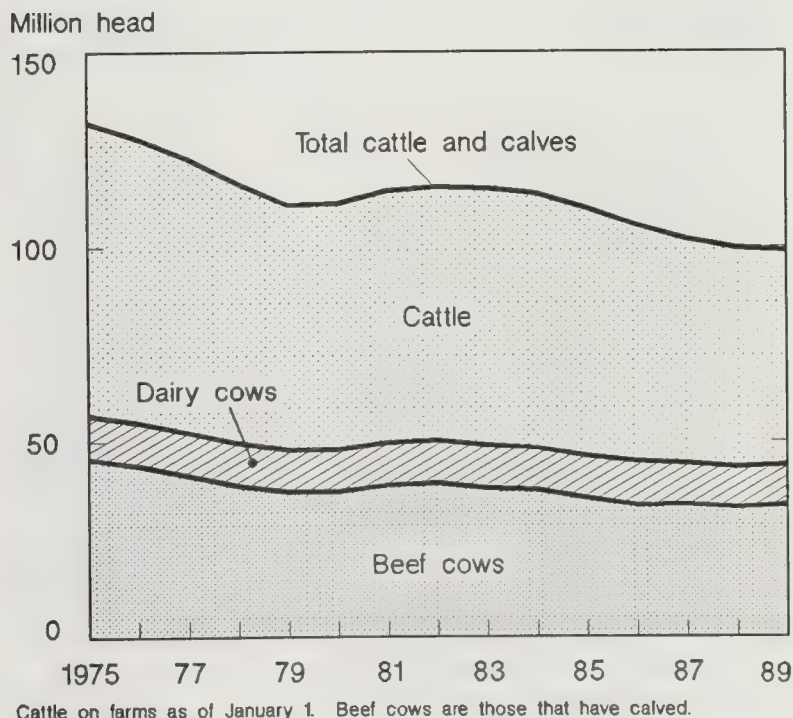


Chart 206
Cattle on farms

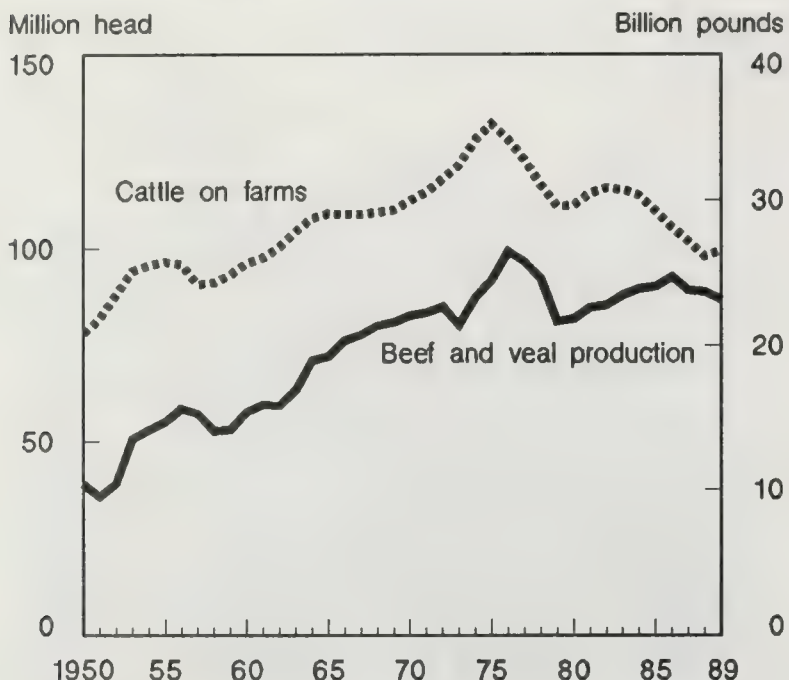


Livestock

Number of cattle rose in 1989 to over 100 million head, while sheep numbers were unchanged at 10.8 million head. Nonfed cattle slaughter will remain down as the cattle inventory begins to increase. Fed cattle marketings and the number of cattle on feed remain large despite the smallest calf crop since the 1960's.

Chart 207

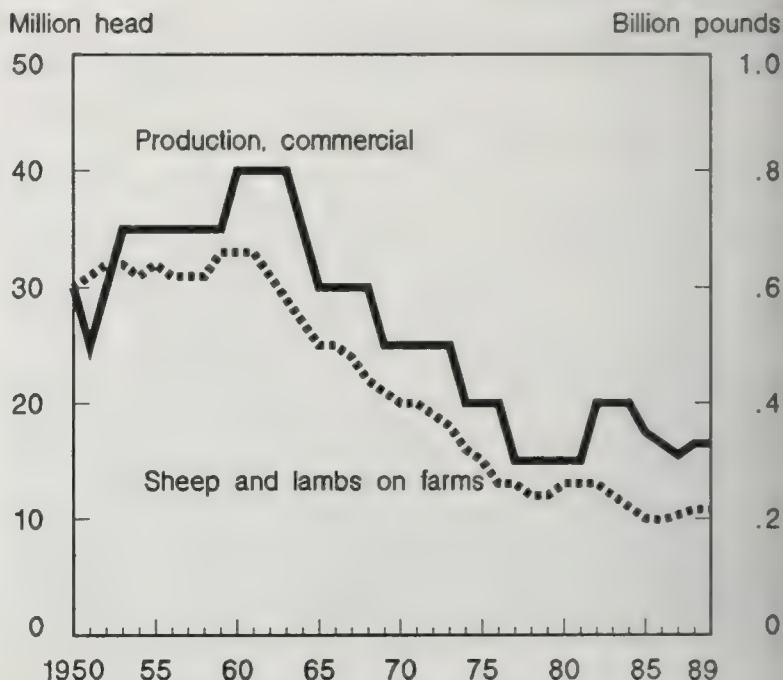
Cattle numbers and beef production



1989 production forecast. Cattle and calves on farms January 1.

Chart 208

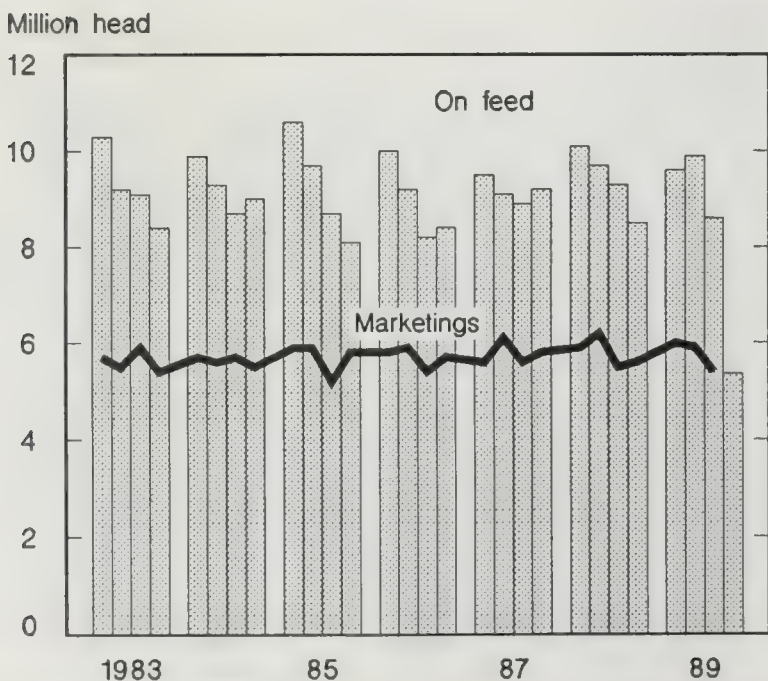
Sheep numbers, lamb and mutton production



1989 production forecast. Sheep and lambs on farms January 1.

Chart 209

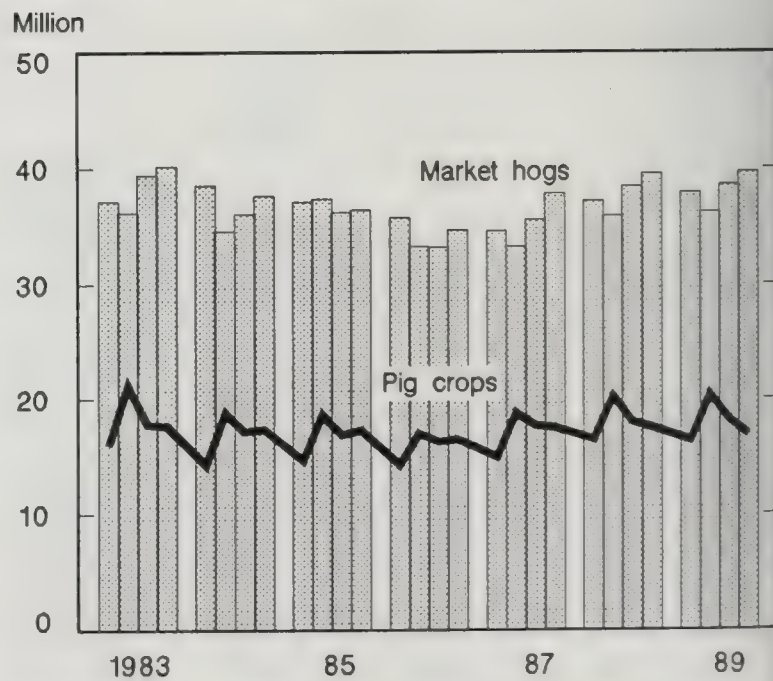
Cattle on feed and marketings



Quarterly data for 13 States.

Chart 210

Market hogs and pig crops



Quarterly data for 10 States.

Livestock

Farm prices for cattle and hogs rose in 1989, while lamb prices declined. Pork production rose 1 percent and retail pork prices were steady. Beef production fell 3 percent, and choice retail beef prices rose 5 percent. Forage problems caused total milk output to slip in 1989.

Chart 211
Fed cattle marketed by feedlot capacity

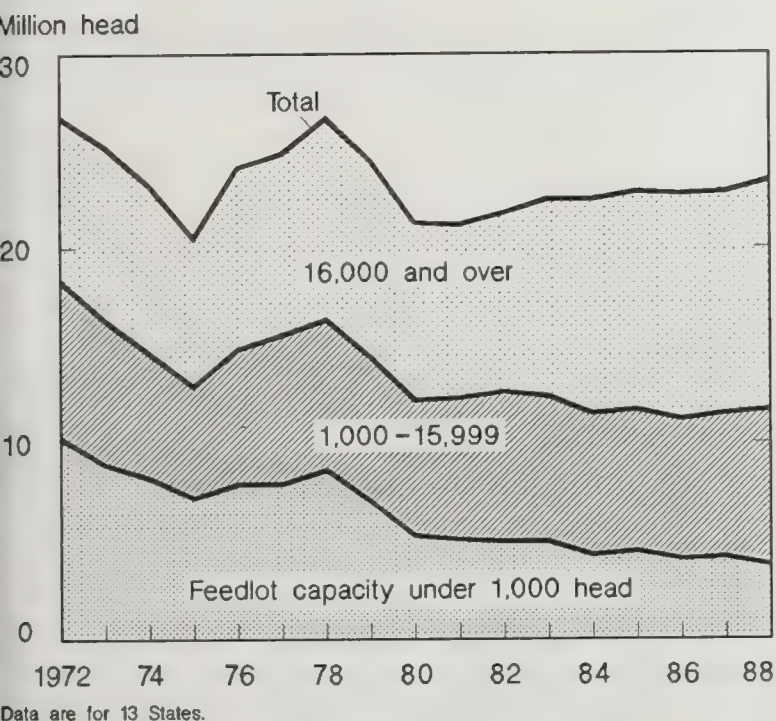


Chart 212
Livestock prices received by farmers

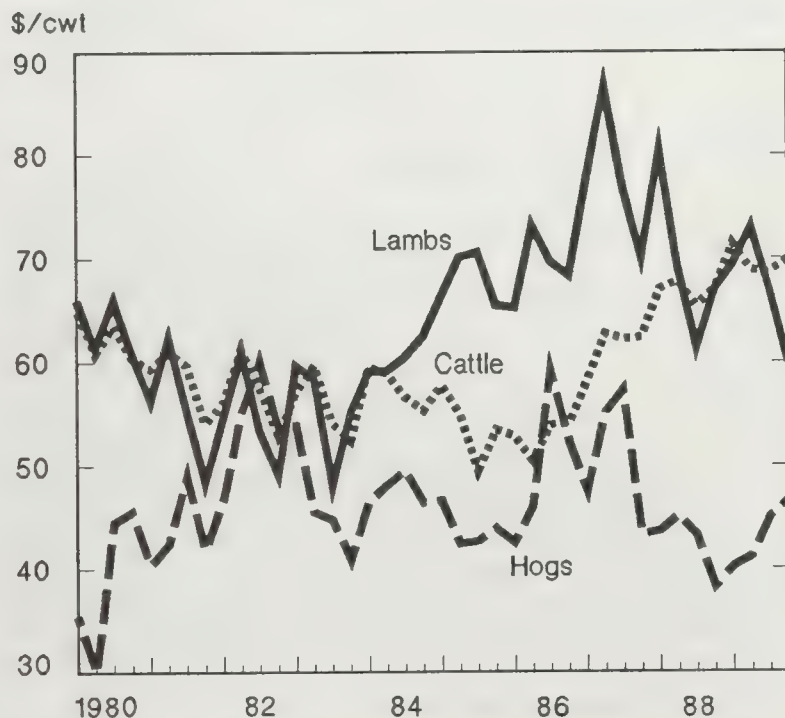


Chart 213
Retail meat prices

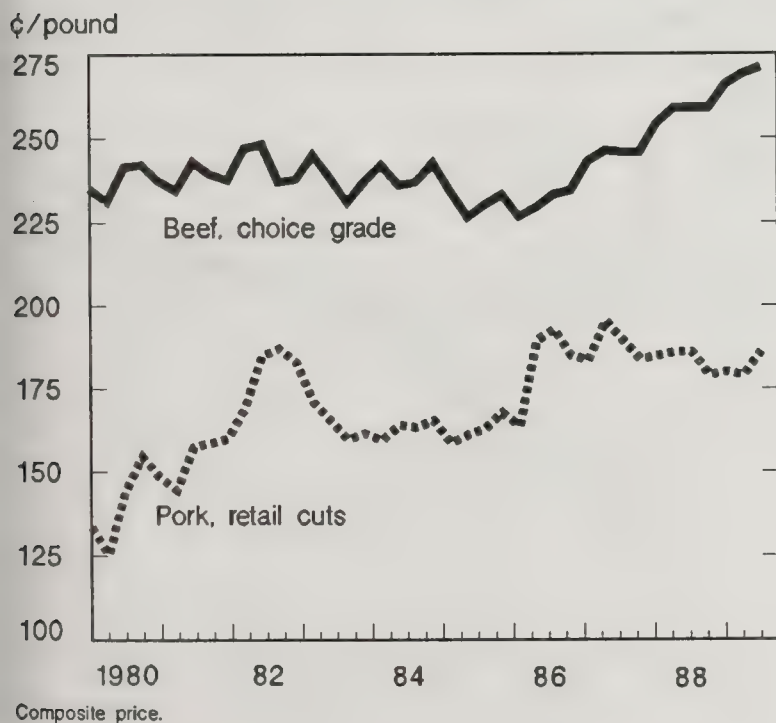
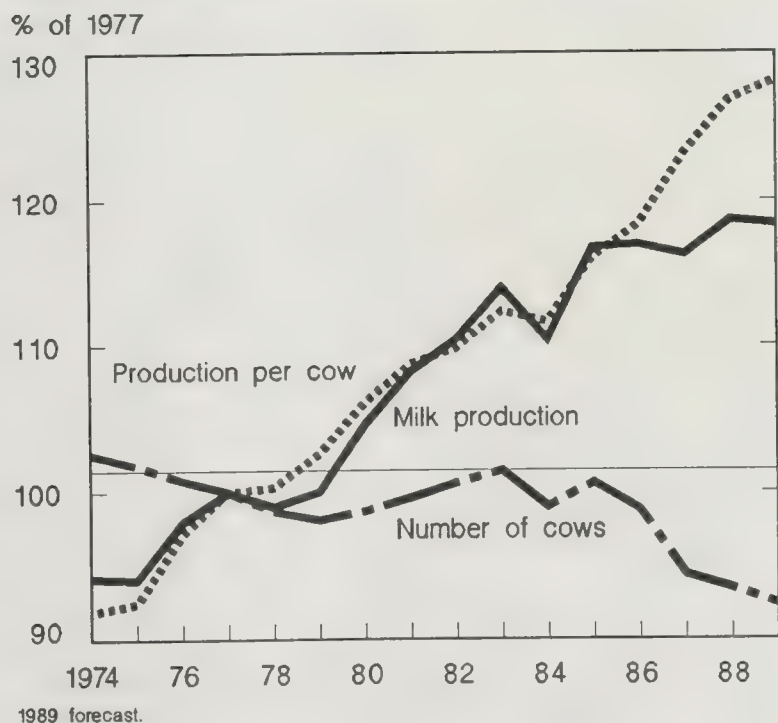


Chart 214
Milk production, number of cows, and milk per cow



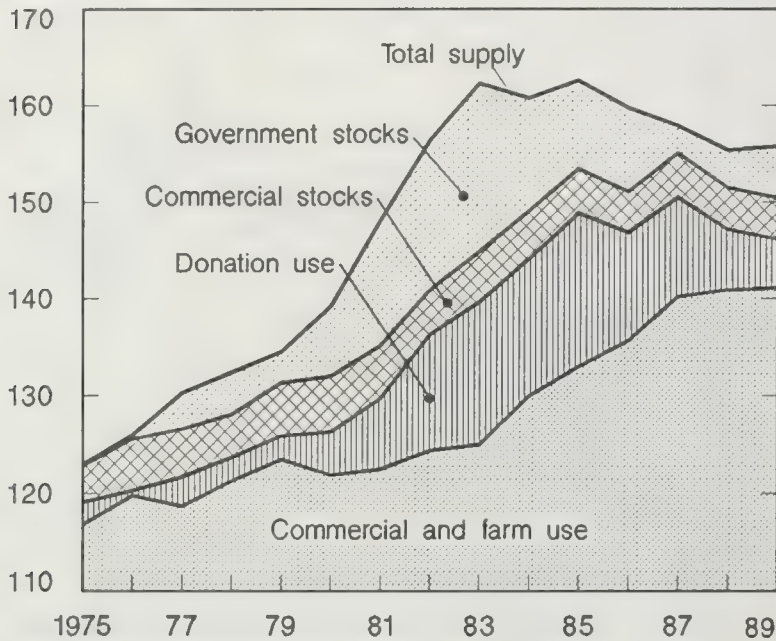
Dairy

Cheese sales continue to outpace sales of other dairy products. 1989 butter purchases by the Commodity Credit Corporation (CCC) stayed high while CCC removals of nonfat dry milk dropped. Retail dairy prices continue to be lower than other prices.

Chart 215

Milk supply, use, and stocks

Billion pounds

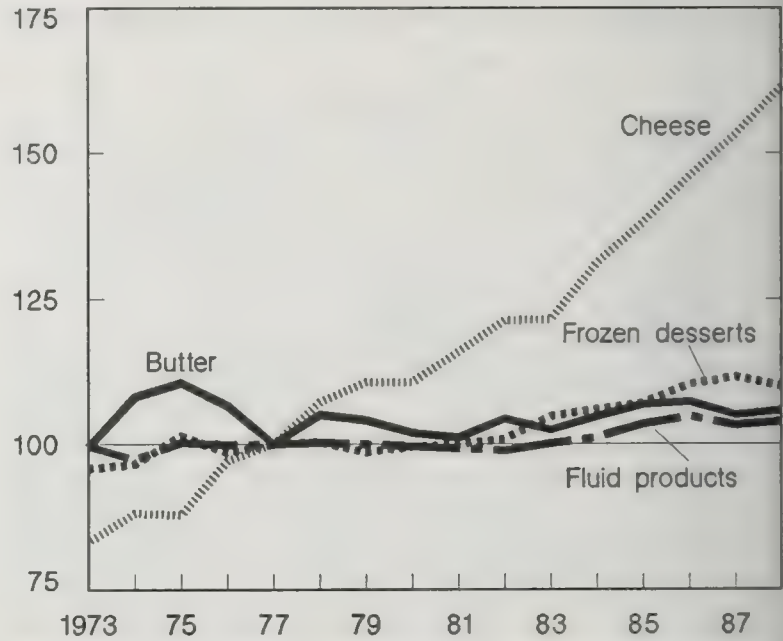


1989 forecast. Stocks as of December 31.

Chart 216

Dairy product sales

% of 1977

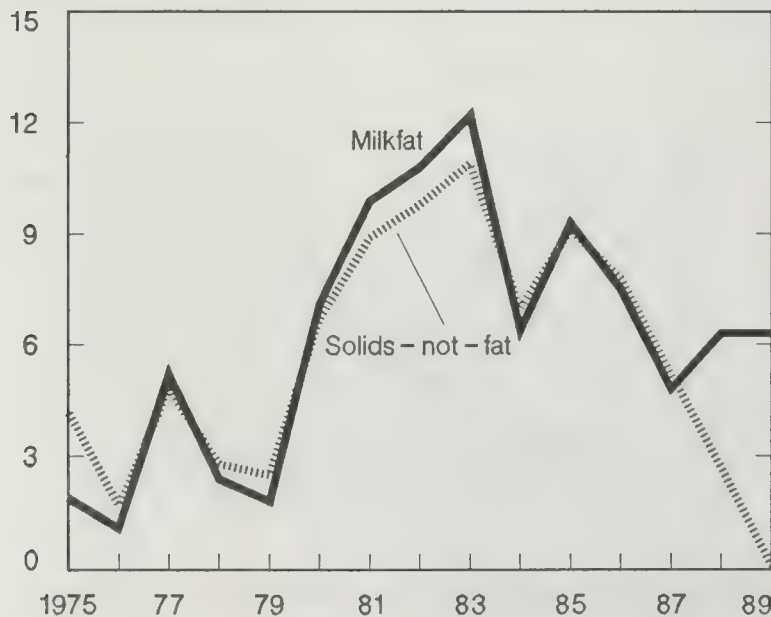


Fluid products include cream and specialty items. Cheese excludes cottage cheese.

Chart 217

Milk solids removed from the market by CCC programs

% of marketings

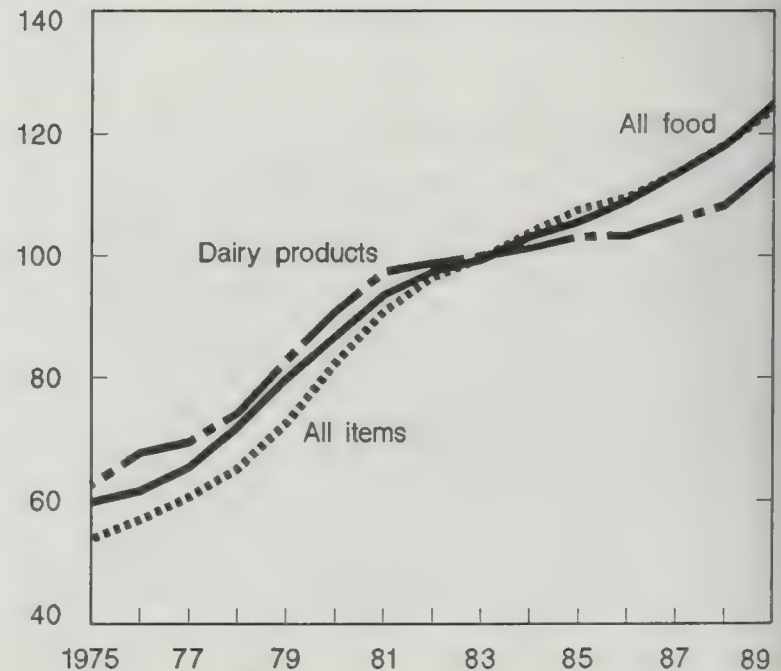


1989 forecast. Deliveries to the Commodity Credit Corporation (CCC) after domestic unrestricted sales.

Chart 218

Consumer price index for dairy products, food, and all items

% of 1982-84



Poultry

Wholesale egg prices rose 30 percent as production dropped in 1989. Layer numbers decreased and the rate of lay remained relatively constant. Production and wholesale prices for broilers and turkeys were higher in 1989.

Chart 219
Eggs: Changes in production and wholesale prices

% change from previous year

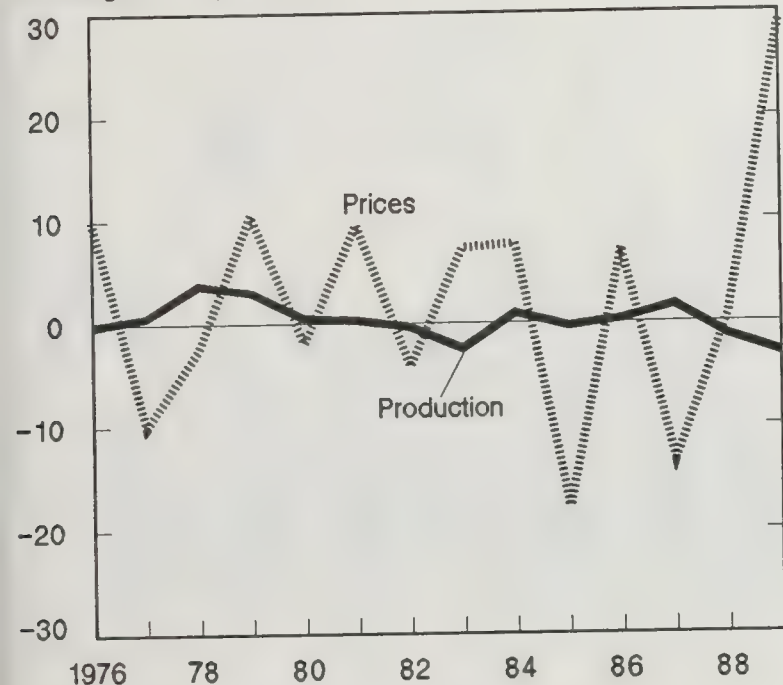
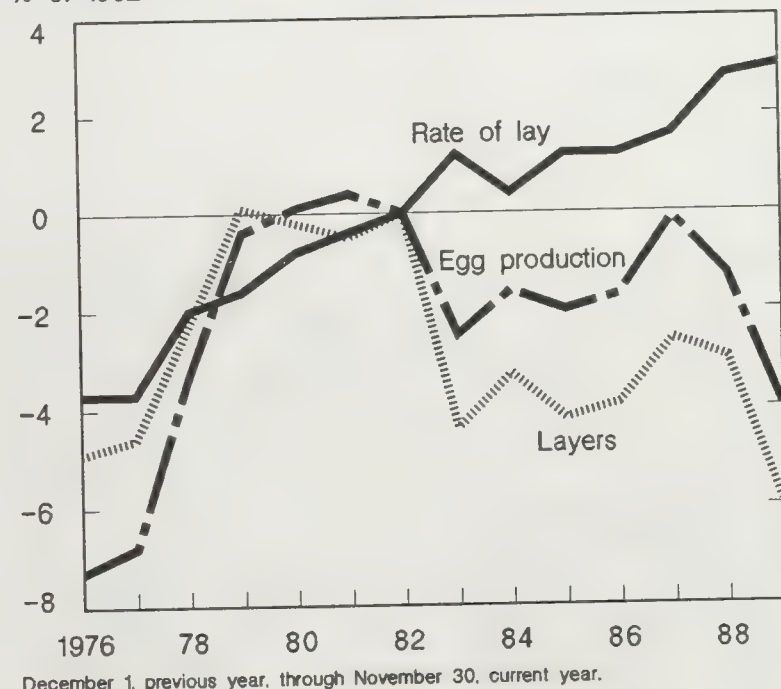


Chart 220
Eggs: Rate of lay, production, and number of layers

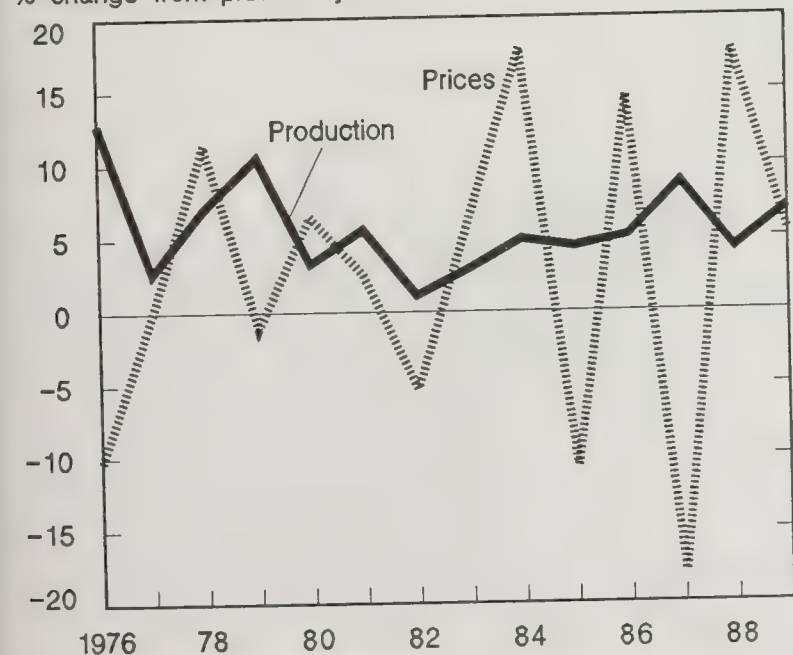
% of 1982



December 1, previous year, through November 30, current year.

Chart 221
Broilers: Changes in production and 12-city wholesale prices

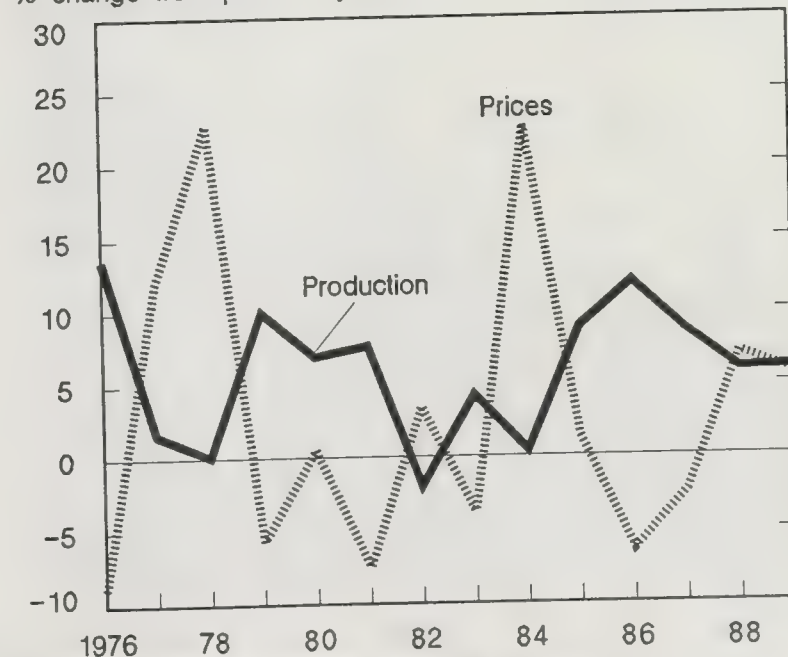
% change from previous year



December 1, previous year, through November 30, current year.

Chart 222
Turkeys: Changes in production and farm prices

% change from previous year



December 1, previous year, through November 30, current year.

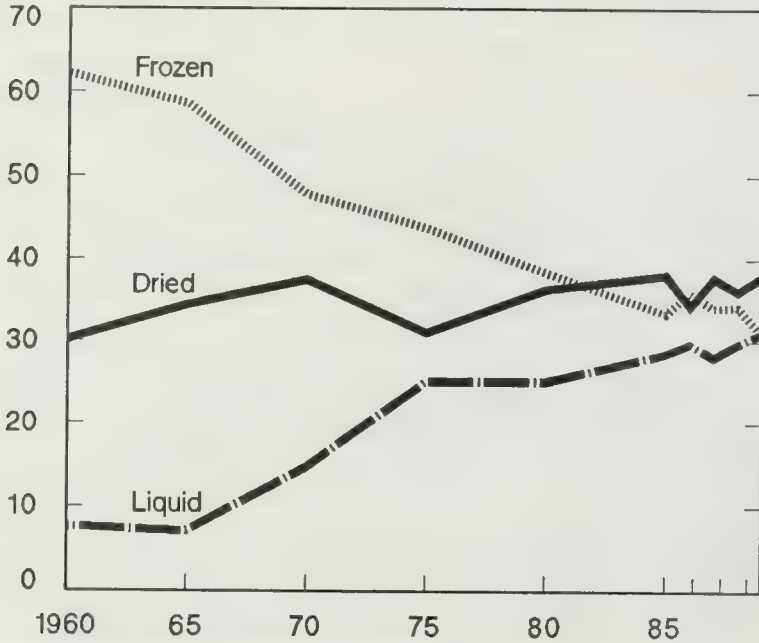
Poultry

1989 third quarter 12-city broiler prices and Eastern region hen turkey prices were lower than 1988 third quarter prices by an average of 9.5 and 14 percent. Liquid and dried egg products represent an increasing share of the egg product use. Total poultry consumption rose, with increases in broiler and turkey consumption of 3.1 and 0.7 pounds per person.

Chart 223

Egg products: Percentage frozen, liquid, and dried

% of total egg products



Liquid eggs are those for immediate consumption.

Chart 224

Wholesale prices: 12-city broilers and New York hen turkeys

¢/pound

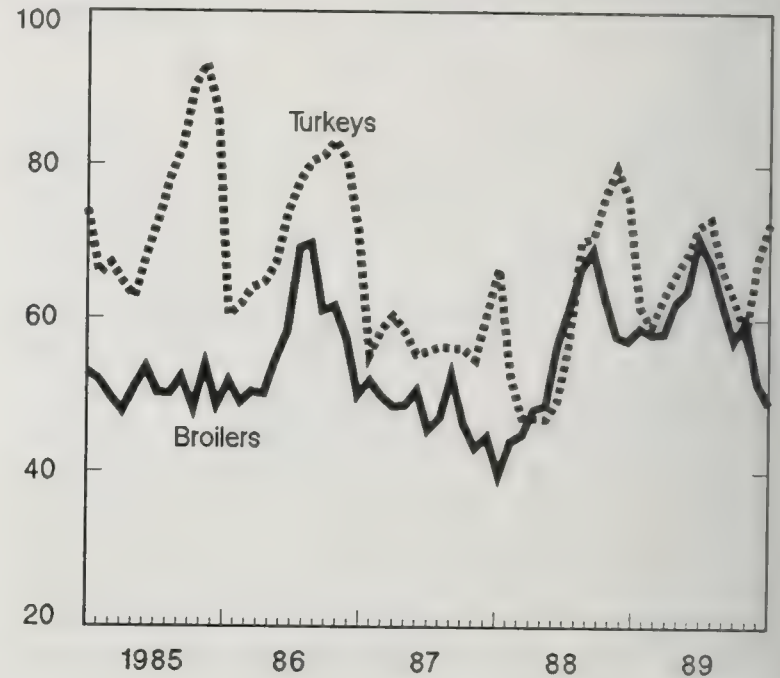
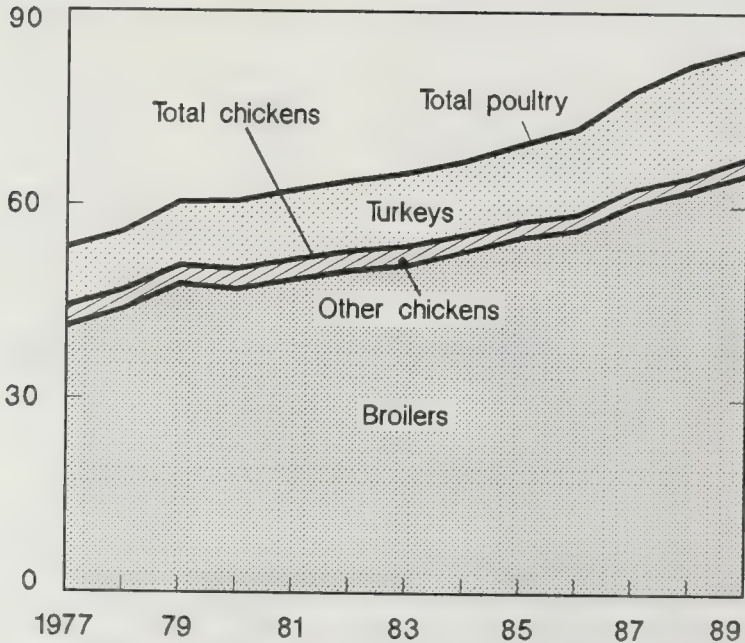


Chart 225

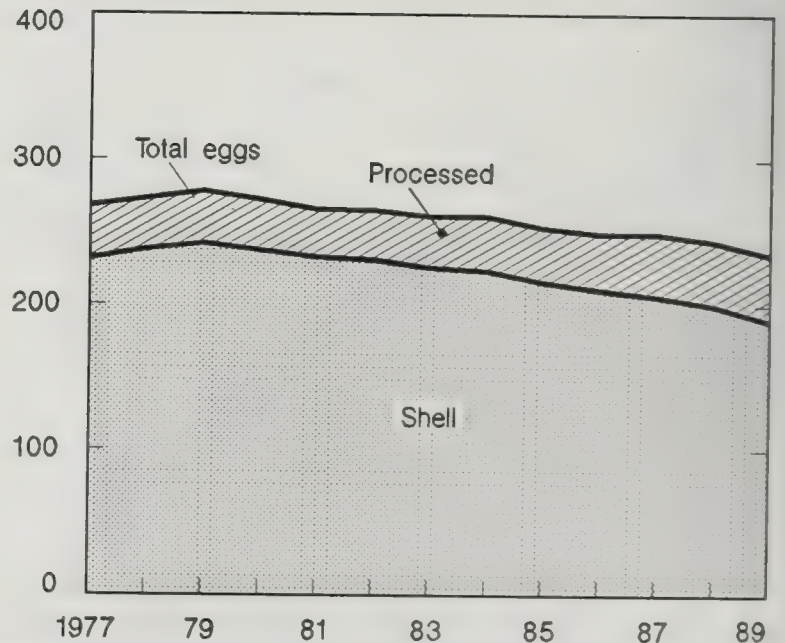
Per capita consumption of poultry and eggs

Pounds of poultry



Poultry is ready-to-cook weight. Eggs are shell eggs plus shell-egg equivalent of egg products.

Number of eggs



Poultry

Broiler exports are increasingly parts rather than whole birds. Most of the increase in turkey consumption has come during the first three quarters rather than being confined to the holiday season.

Chart 226
**Turkey consumption trends:
Total and fourth/quarter**

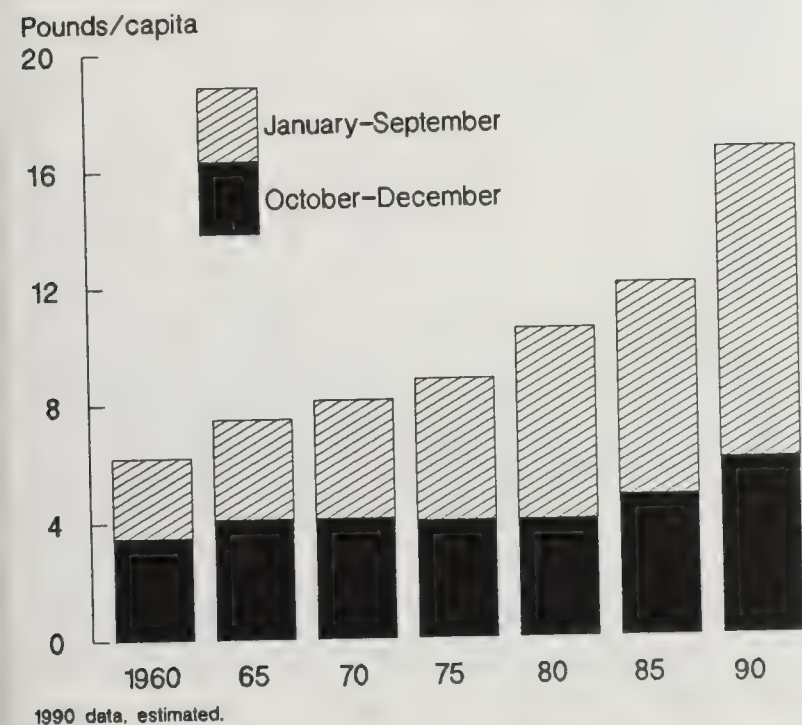


Chart 227
Broilers: Whole bird and parts exports

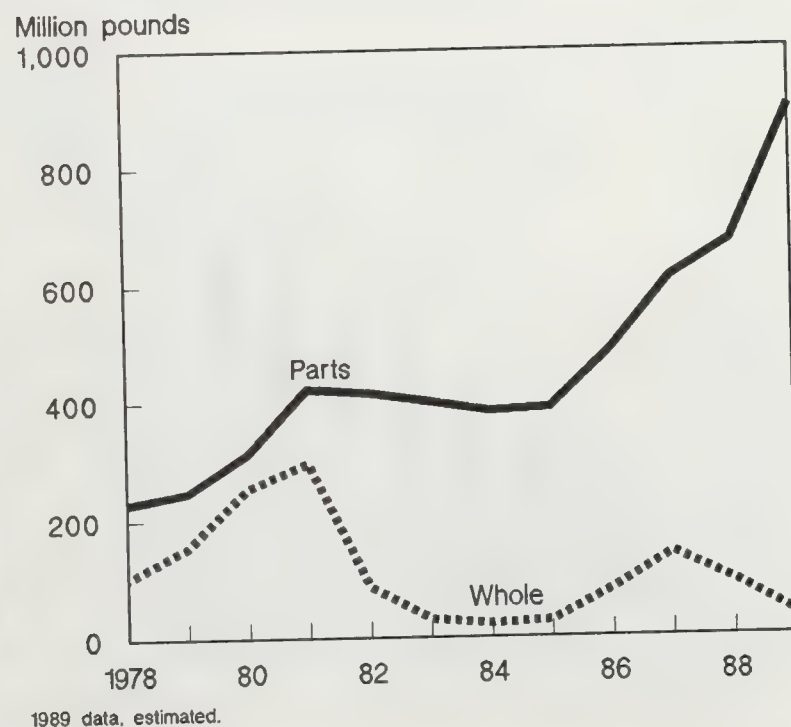
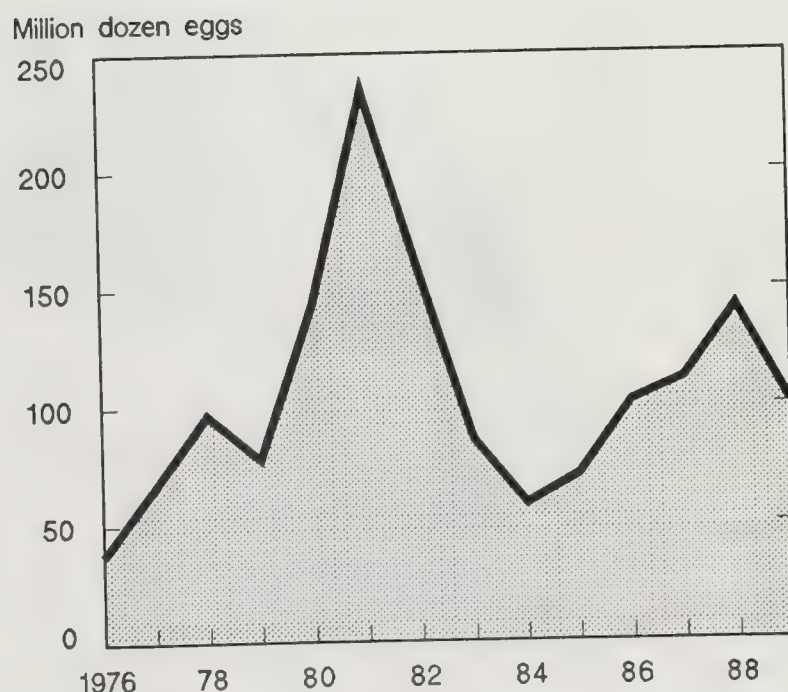
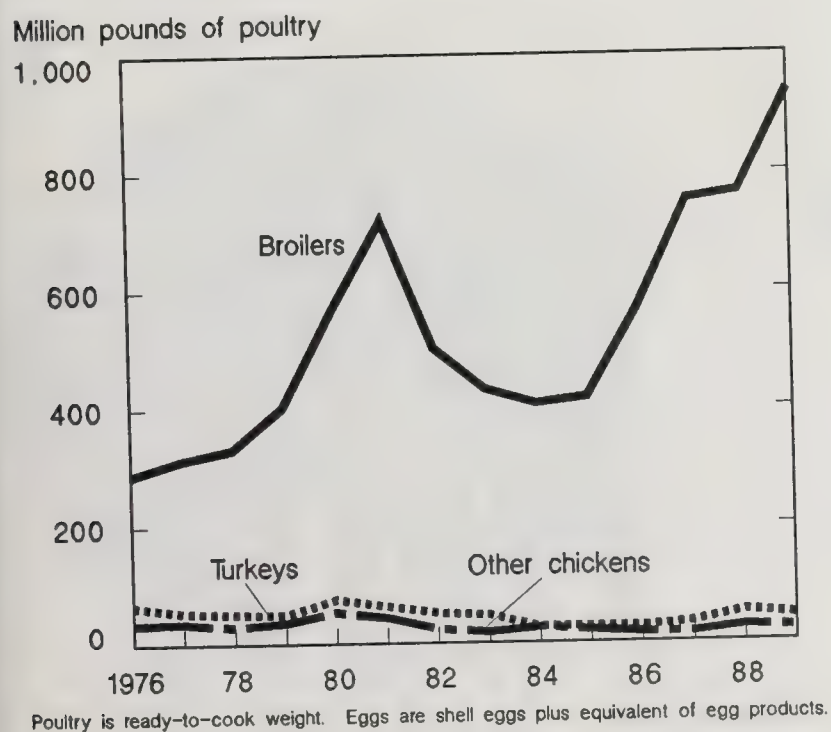


Chart 228
U.S. exports of poultry products



Aquaculture

Domestic production of fish and shellfish increased about 40 million pounds in 1988, most of the growth coming from catfish producers. Even so, the growth rate in the catfish industry was lower than in previous years. Catfish delivered to processors totaled 295 million pounds in 1988, up 5 percent from 1987.

Chart 229
U.S. aquacultural production

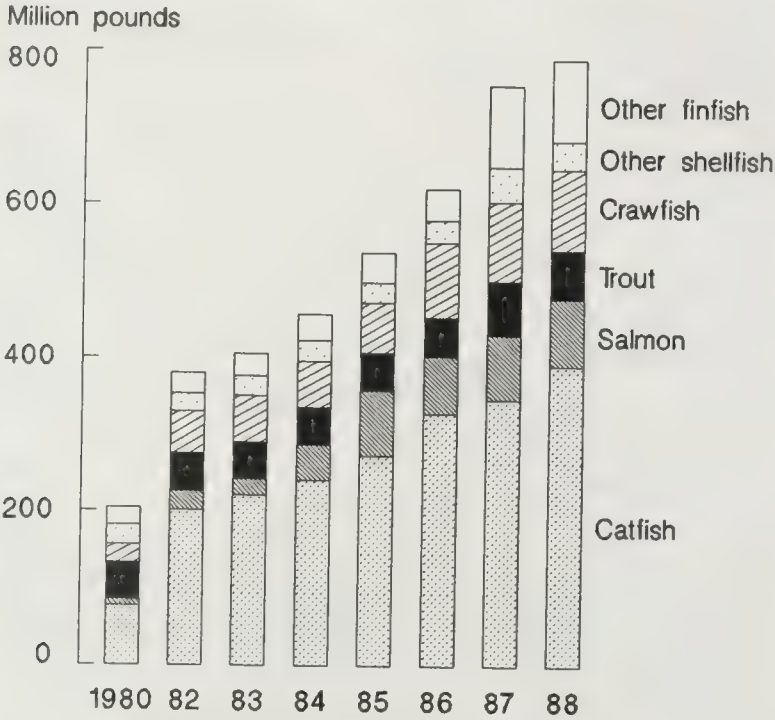


Chart 230
U.S. production of catfish delivered to processors

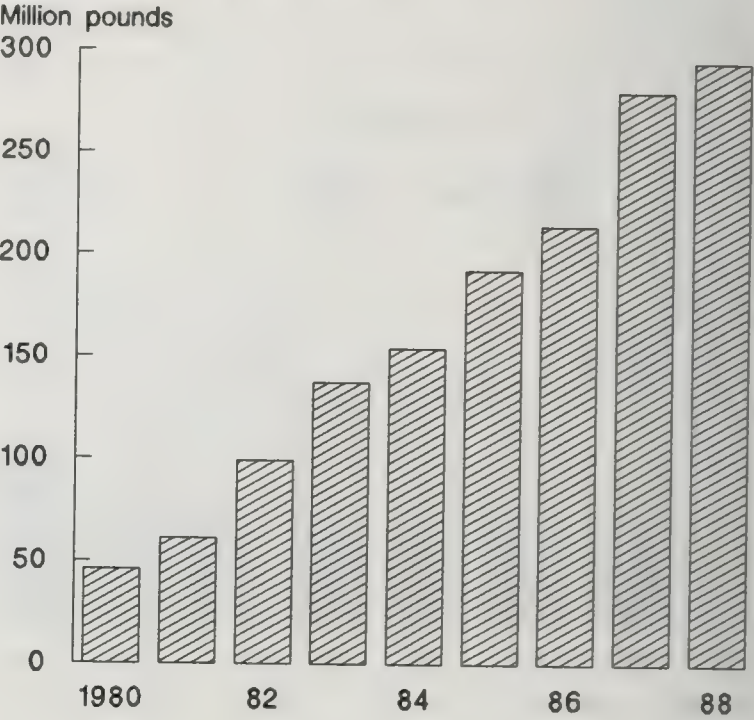
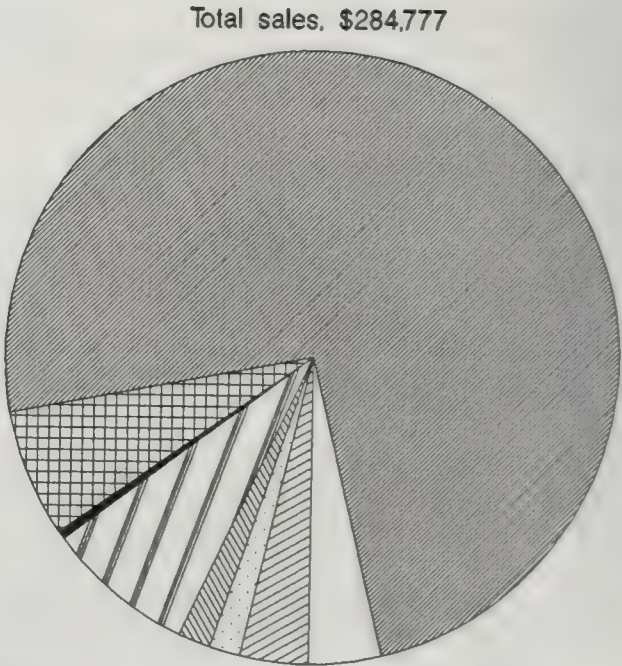
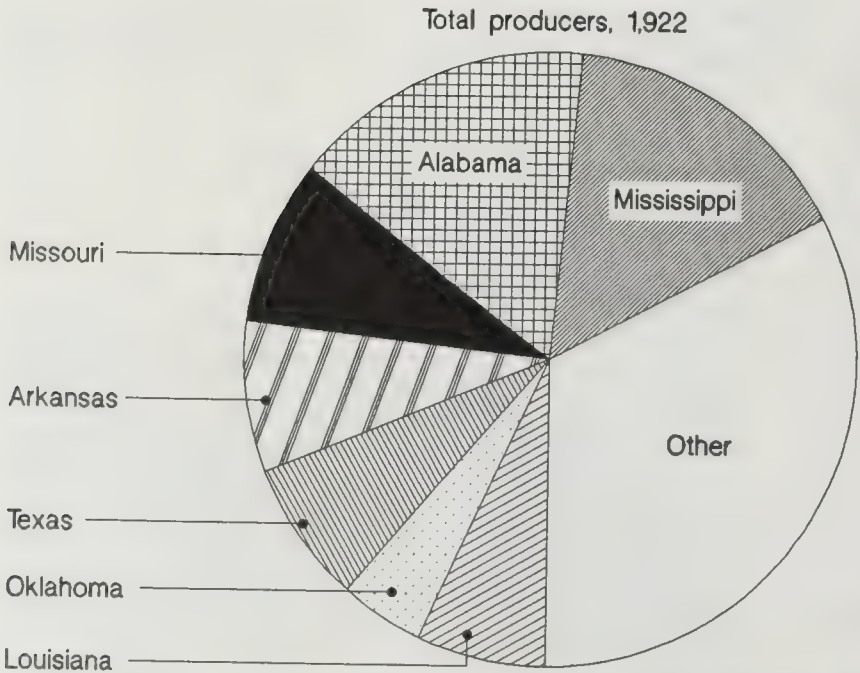


Chart 231
Number of U.S. catfish producers and total sales by State, 1988



Other includes California, Florida, Georgia, Kentucky, South Carolina, Tennessee, Idaho, Indiana, Illinois, and Kansas.

Rice and Other Grains

U.S. rice production declined 2 percent from the 1988/89 level. Record yields were reported in 1989/90, but harvested acreage was 5 percent below 1988/89. U.S. carryin stocks for 1989/90 were the lowest since 1980/81. World rice production is expected to reach record levels in 1989. World coarse grain exports recorded first substantial growth since 1985 lows.

Chart 232
U.S. rice acreage, yield, and production

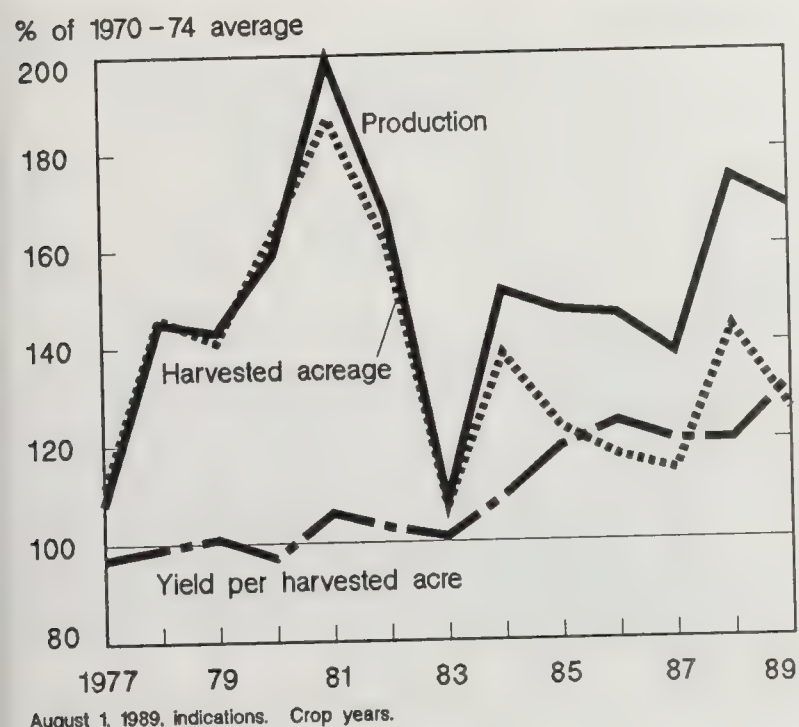


Chart 233
U.S. rough rice supply and use

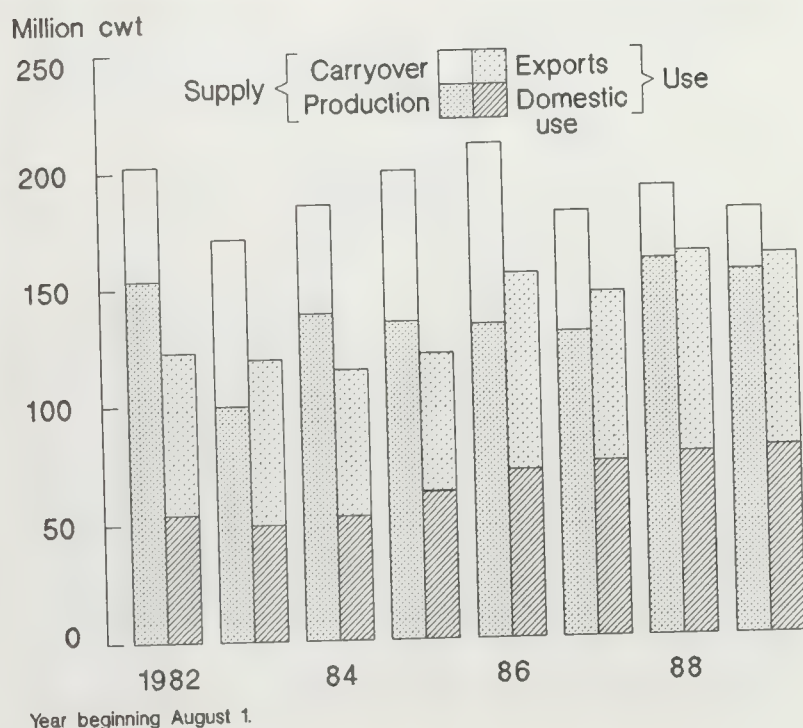


Chart 234
Major rice producers

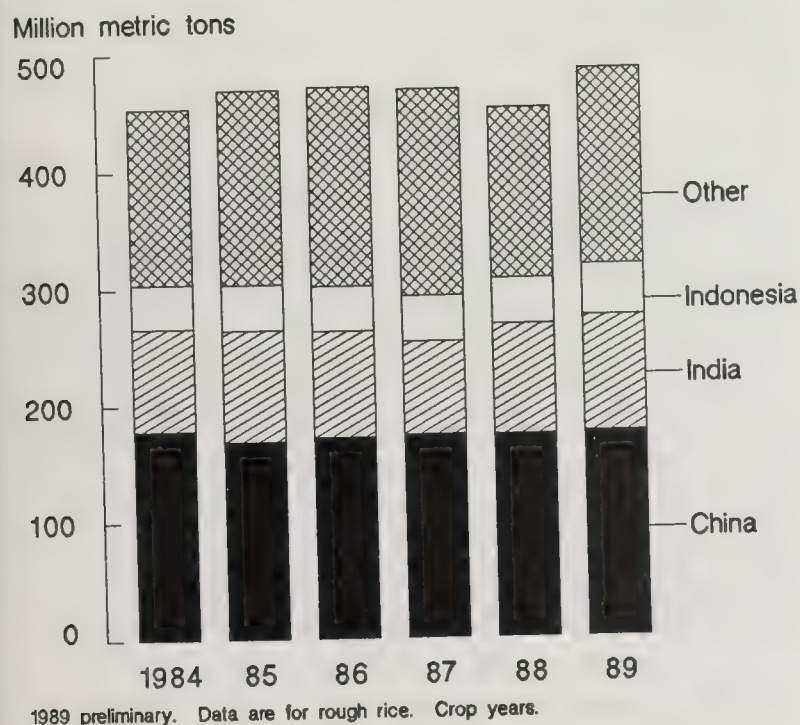
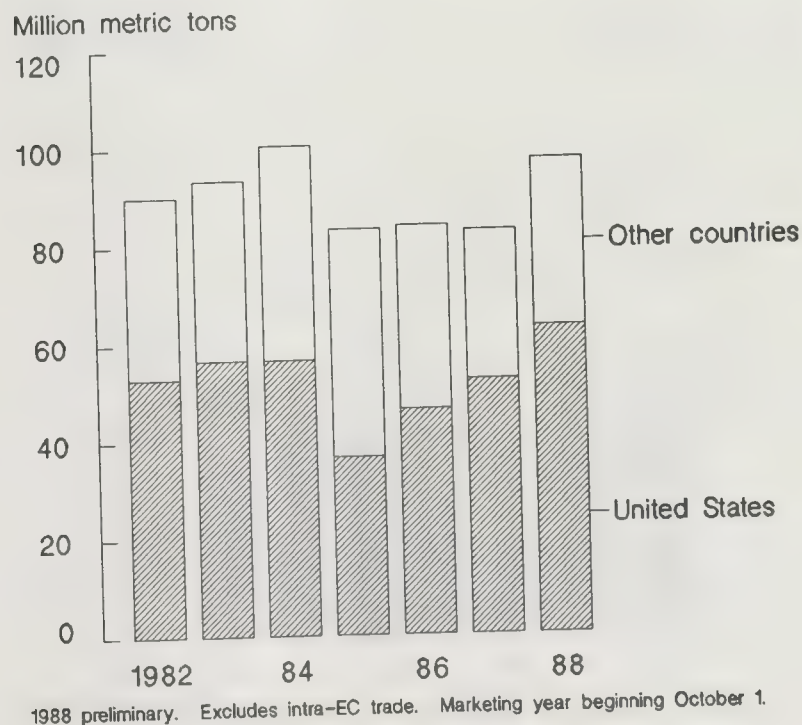


Chart 235
World exports of coarse grains



Wheat

Drought reduced 1989 U.S. wheat yields below 1988 levels. U.S. wheat exports are expected to decline in 1989/90, while world wheat exports are expected to rise. U.S. shipments to Asia continue to increase.

Chart 236

U.S. wheat acreage, yield, and production

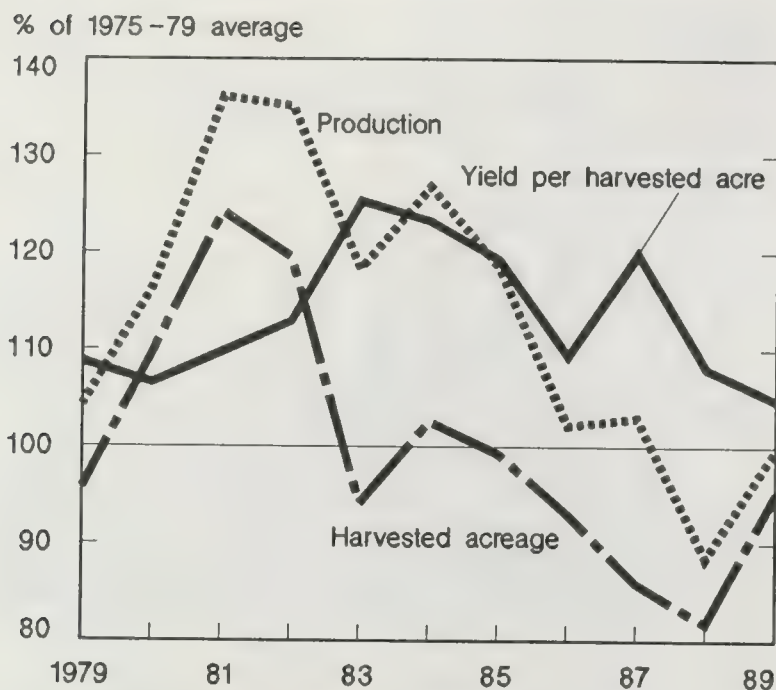


Chart 237

U.S. wheat supply and use

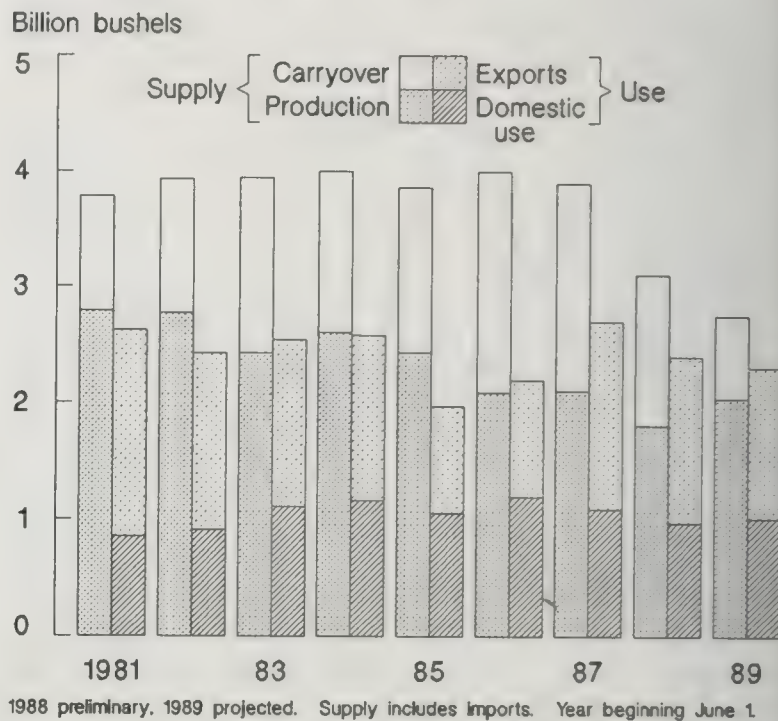


Chart 238

Major wheat exporters

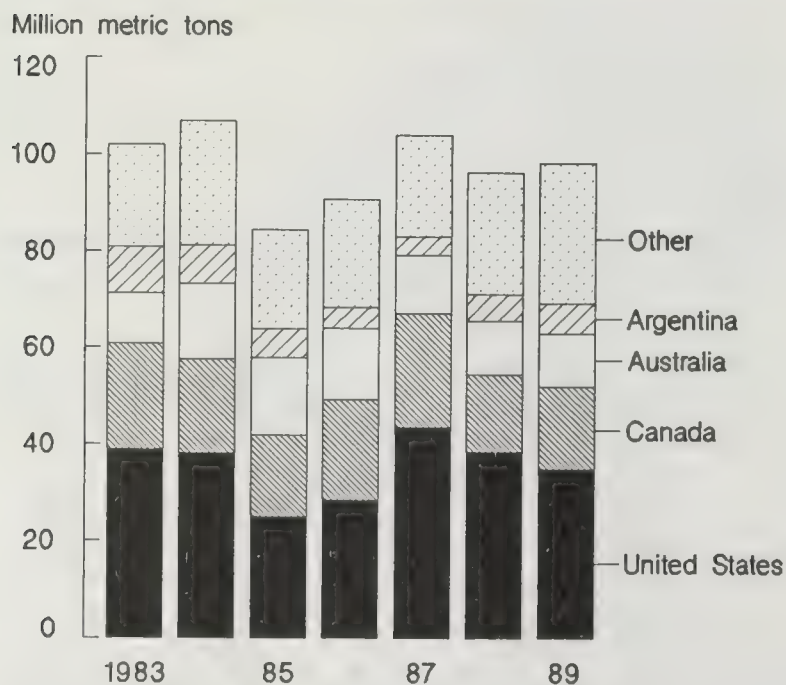
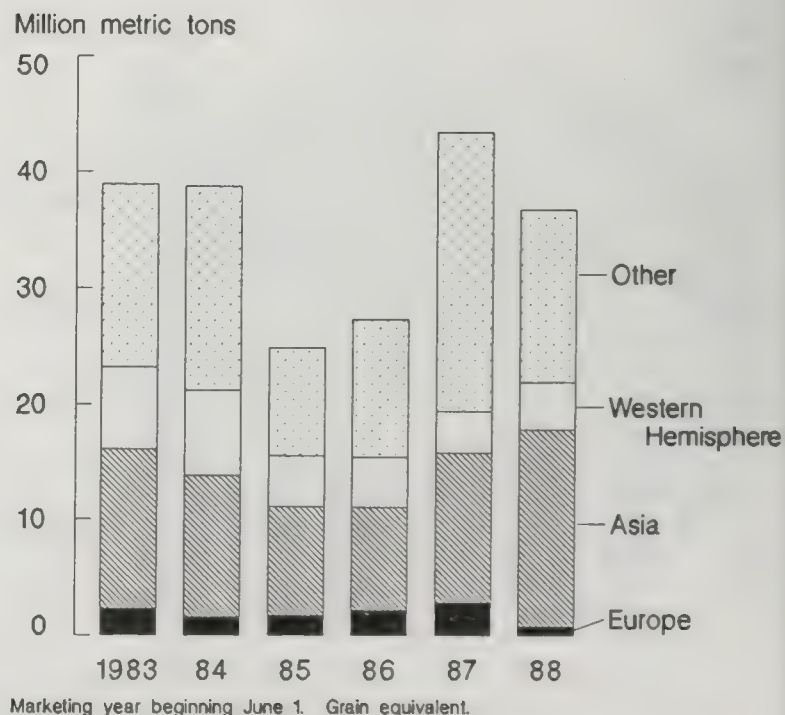


Chart 239

Destination of U.S. wheat exports



Coarse Grains

Corn supplies are expected to be up 4 percent from 1988/89. Larger supplies will likely lower prices, helping to increase domestic use. Feed concentrate use may be up from 1988/89, but not back to previous high levels mainly because of the increase in nonfeed uses of corn.

Chart 240
U.S. corn prices

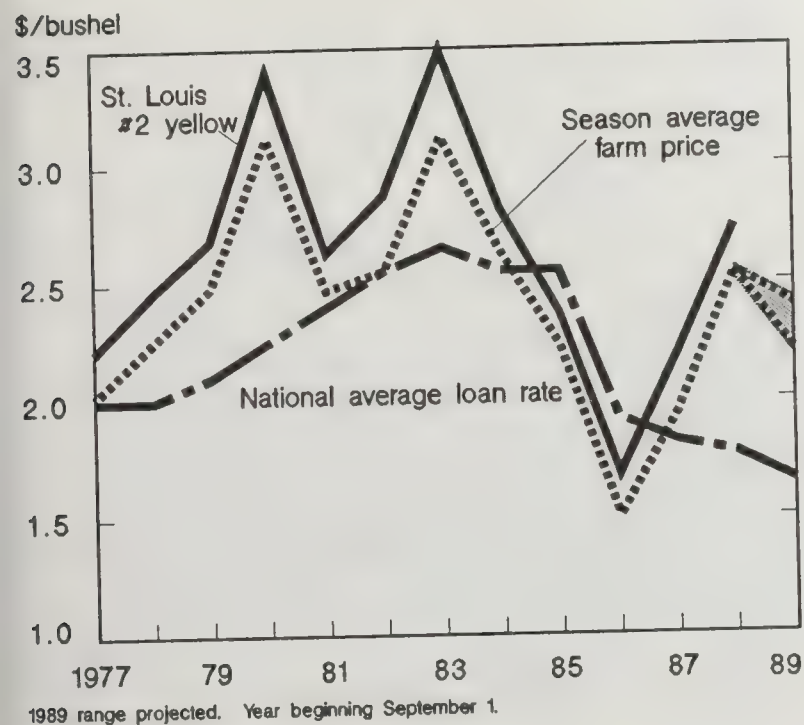


Chart 241
U.S. corn supply and use

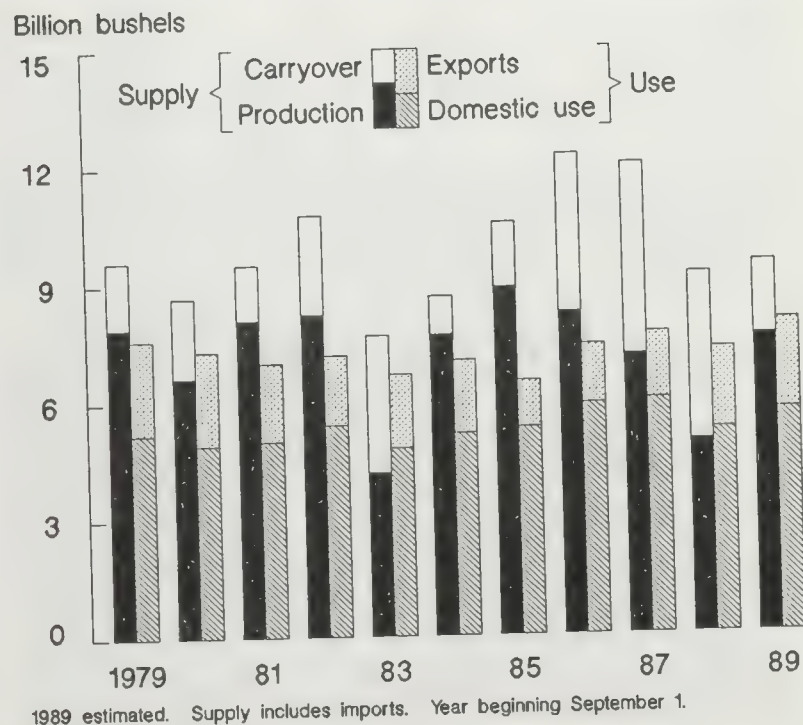


Chart 242
Feed concentrates fed to livestock and poultry

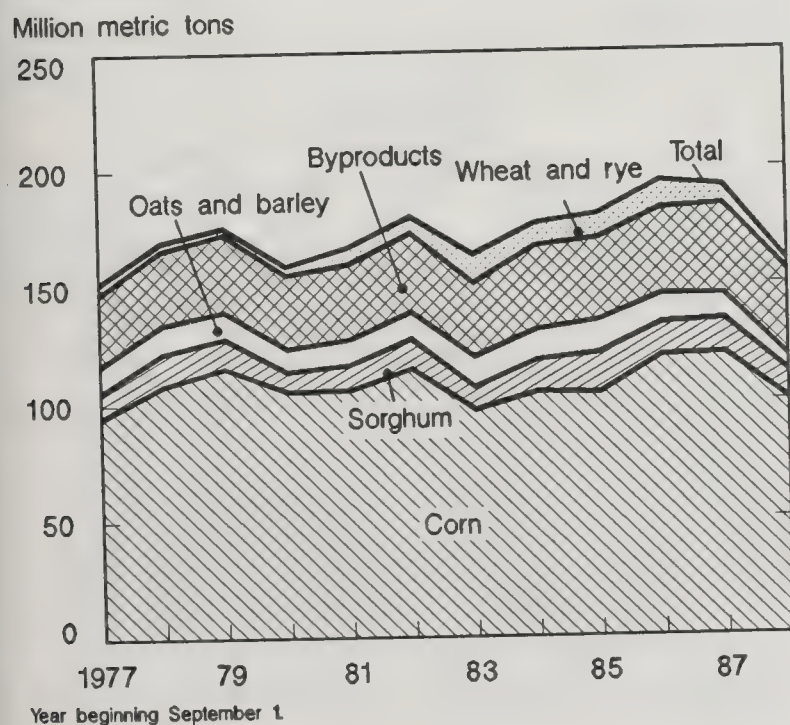
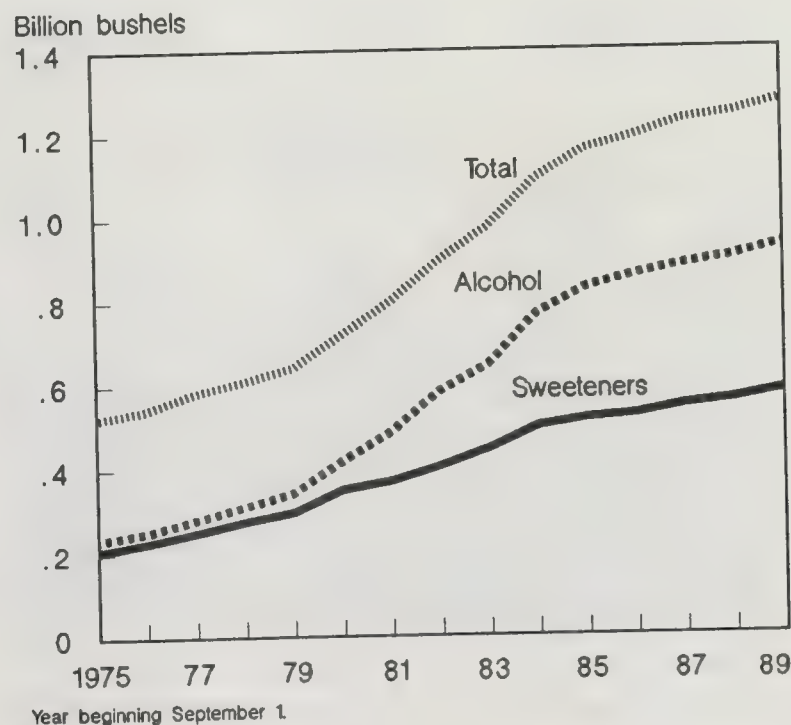


Chart 243
Food, seed, and industrial use of corn



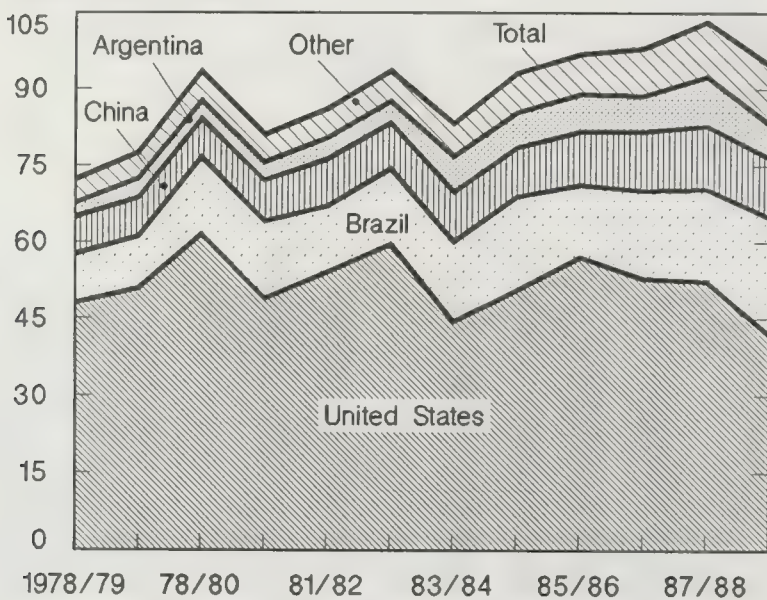
Soybeans

World soybean production dropped 8 percent due to droughts in the United States and Argentina. The value of U.S. soybean and product exports was \$6.9 billion in 1988, up 21 percent. U.S. soybean exports totaled 21.9 million metric tons in 1987/88, up nearly 6 percent. End-of-year carryover dropped for the fourth consecutive year.

Chart 244

Major soybean producers

Million metric tons

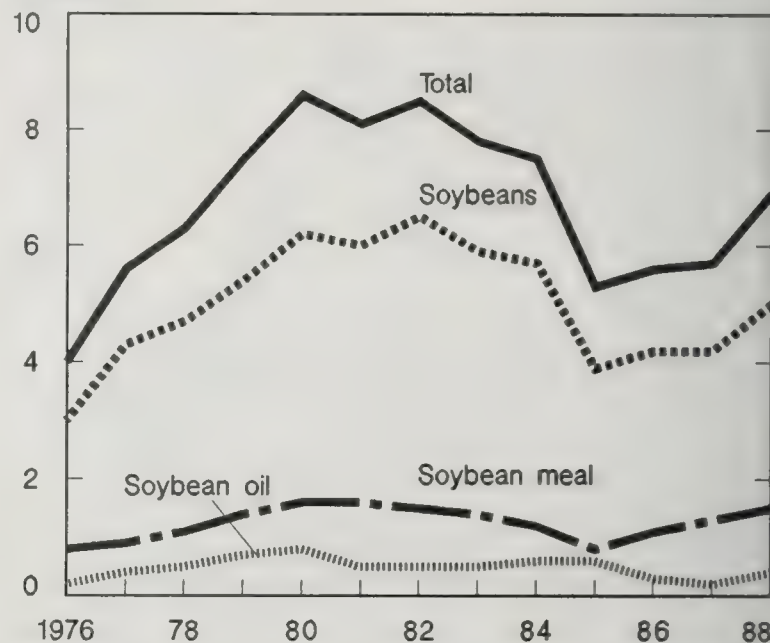


1988/89 preliminary. Soybean production split year includes Northern Hemisphere crops harvested in the last months of the first year shown and Southern Hemisphere crops harvested early in the following year.

Chart 245

Value of U.S. exports of soybeans and products

\$ billion

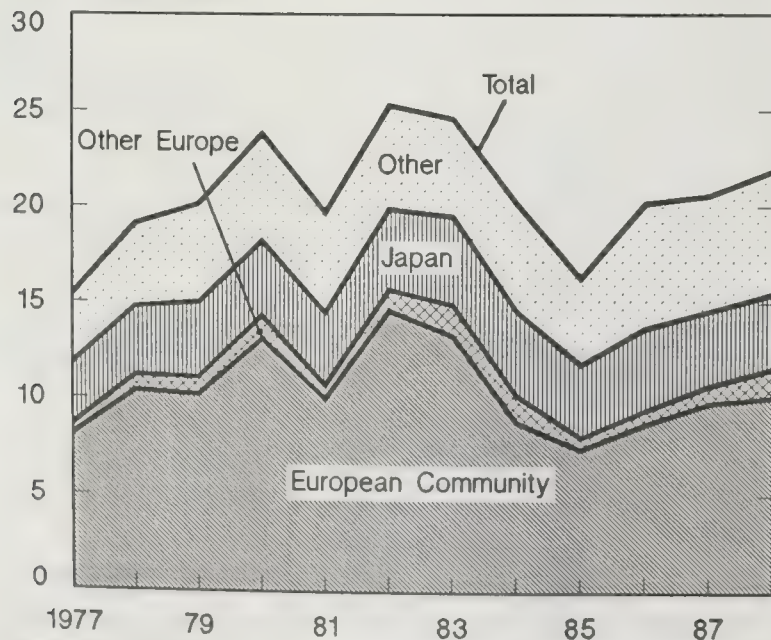


Fiscal years.

Chart 246

Destination of U.S. soybean exports

Million metric tons

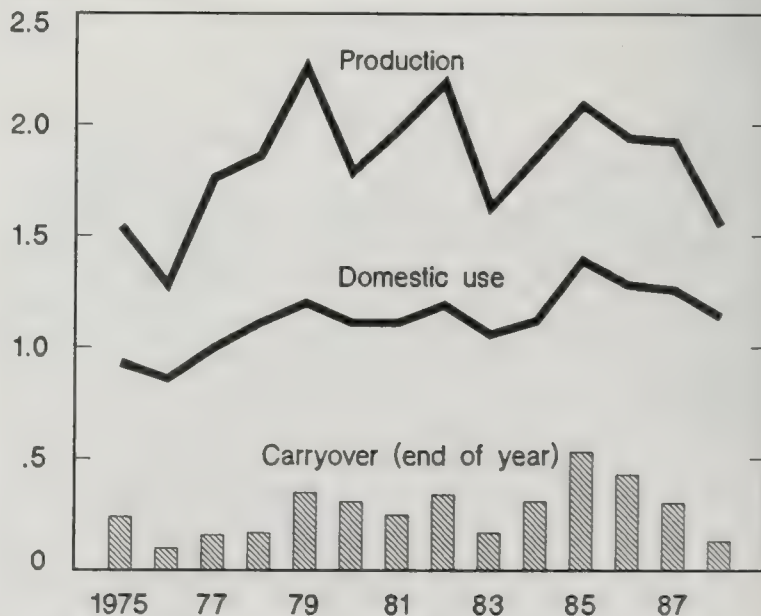


Marketing year September–August. Other includes Canada and the Soviet Union.

Chart 247

U.S. soybean production, use, and carryover

Billion bushels

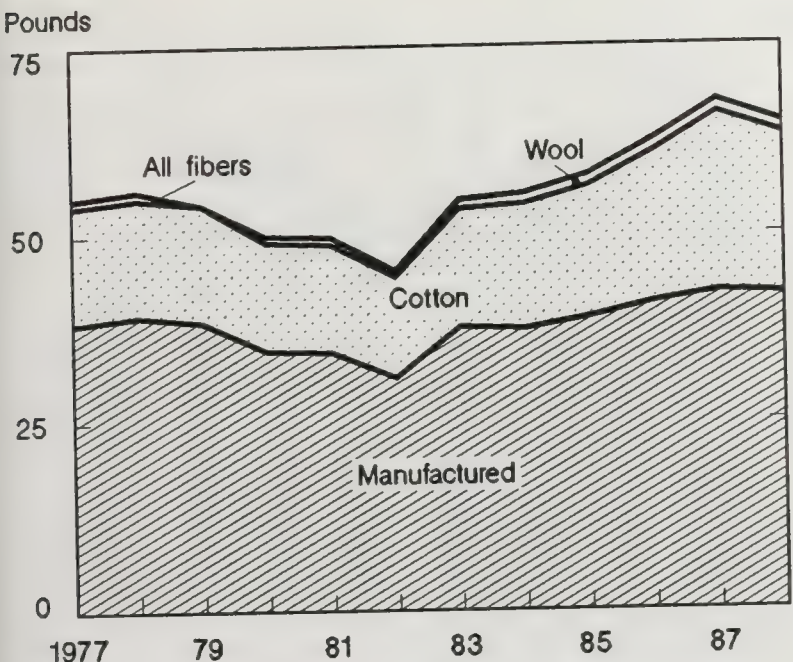


Domestic use includes crushings, seed, feed, and residual. Year beginning September 1.

Fibers

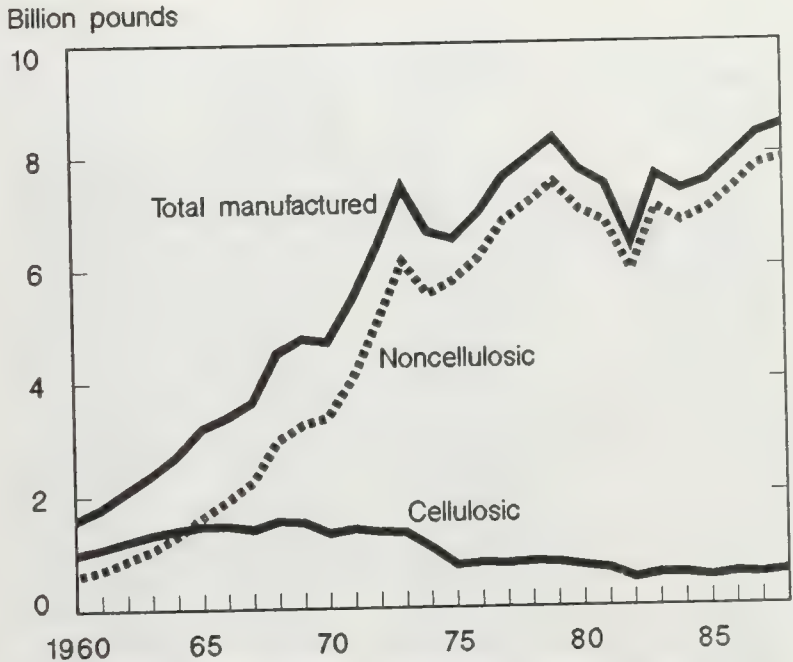
U.S. per capita domestic consumption of all fibers was almost 65 pounds, down 4 percent from 1987. U.S. cotton production in 1989/90 is forecast 22 percent lower than the year before. Exports are expected to rise 26 percent. U.S. exports declined by 332,000 bales in 1988, due, in part, to a buildup of stocks. Foreign exports increased 2.7 million bales as demand increased for cheaper foreign cotton.

Chart 248
U.S. per capita consumption of fibers



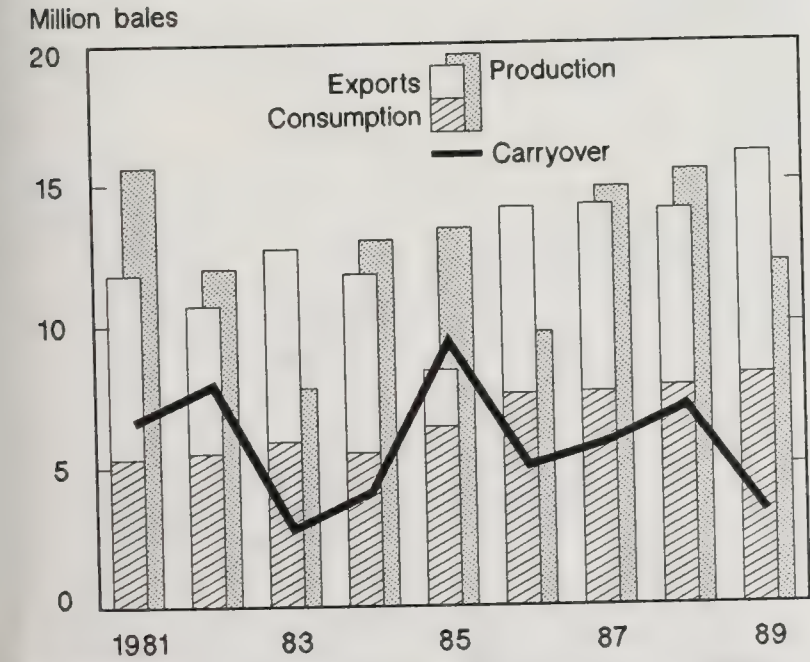
1988 preliminary. Mill consumption adjusted for fiber equivalent of trade balance in textile manufactures. All fibers do not include flax and silk.

Chart 249
U.S. shipments of manufactured fiber



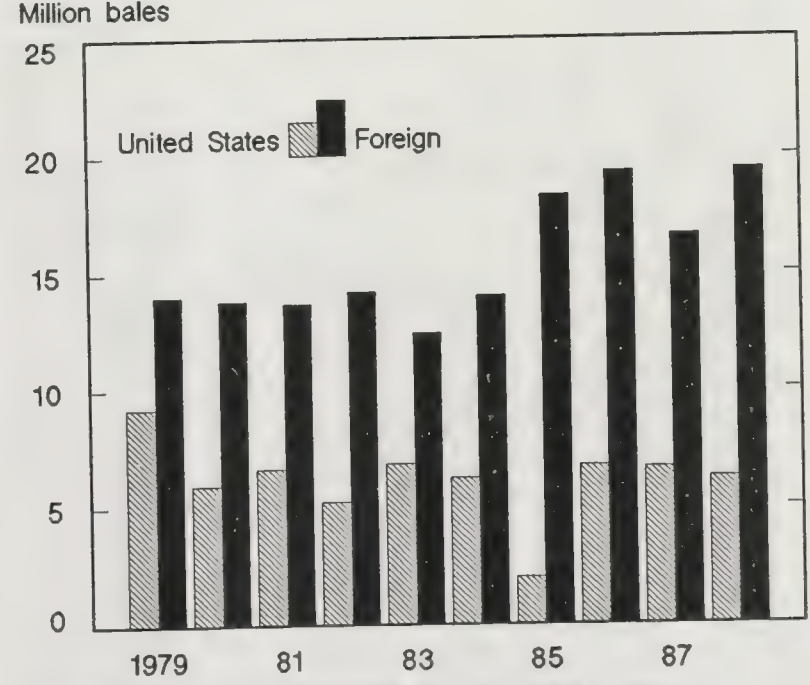
Nylon, polyester, acrylic, olefin, glass, and spandex are noncellulosic fibers. Rayon and acetate are cellulosic fibers. Shipments to domestic customers.

Chart 250
U.S. cotton production, use, and carryover



1989 preliminary. Bales of 0.218 metric tons (480 pounds net). Year beginning August 1. Ending carryover.

Chart 251
World cotton exports



Bales of 0.218 metric tons (480 pounds net). Year beginning August 1.

Fibers

U.S. cotton production showed a 651,000-bale gain over 1987 levels as larger acreage more than offset lower yields. World consumption held steady in 1988. Lower domestic consumption levels and larger domestic production of raw wool in 1988 led to lower raw wool imports. World raw wool demand and production continued strong in 1988.

Chart 252

World cotton production and consumption

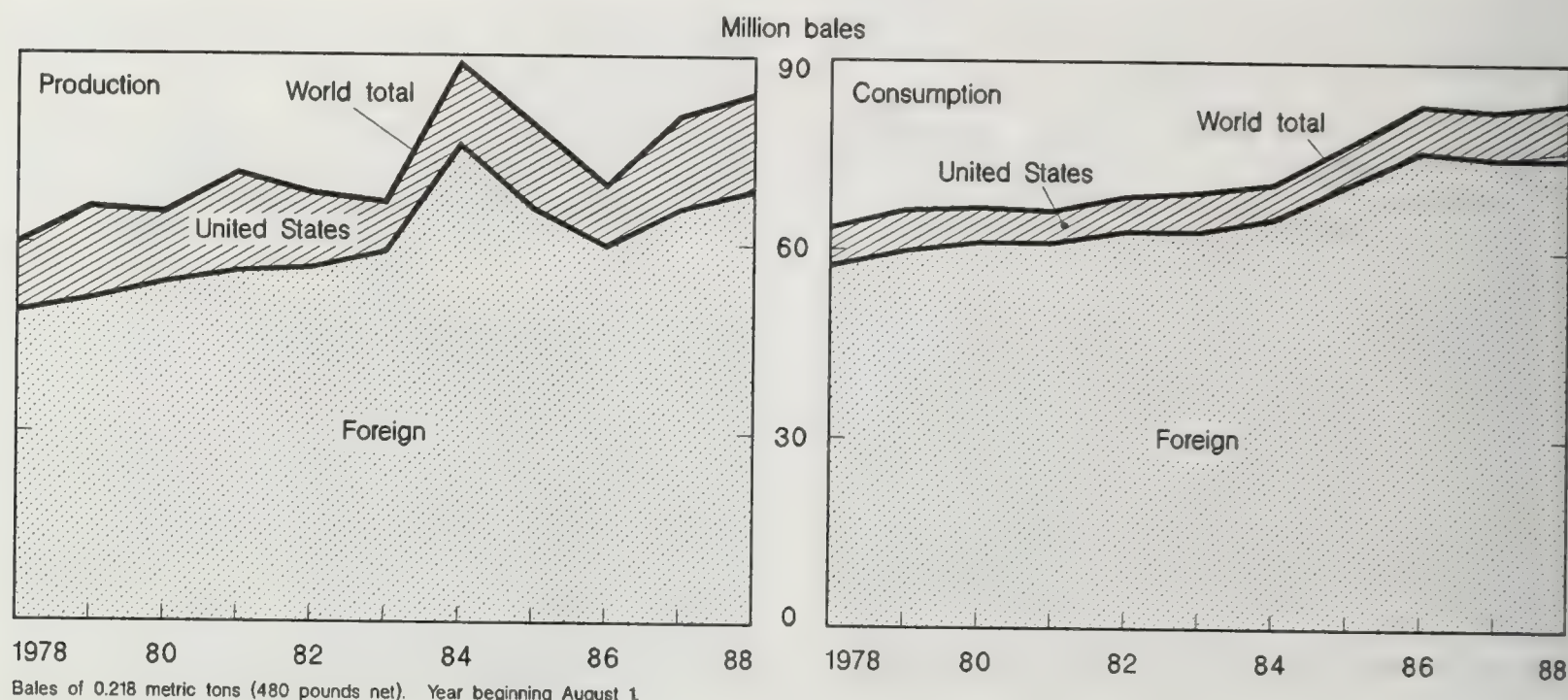
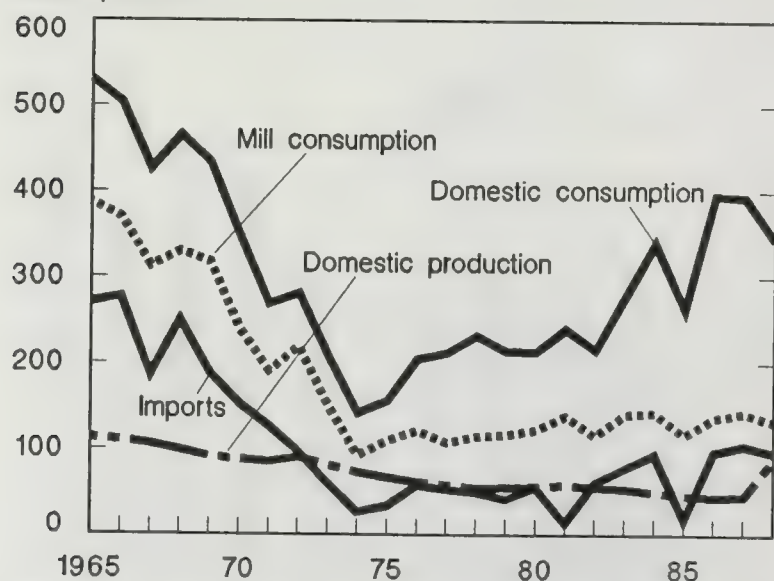


Chart 253

U.S. production, imports, and consumption of raw wool

Million pounds

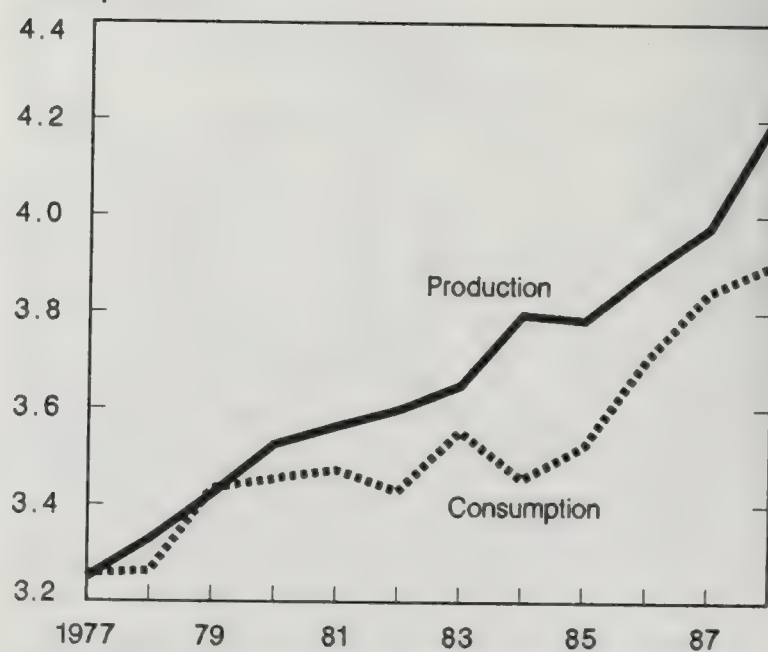


Clean basis. Production includes shorn and pulled wool. Imports include duty-free and dutiable wool. Mill consumption includes apparel and carpet wool. Domestic consumption includes mill consumption plus raw wool equivalent of net textile trade balance.

Chart 254

World production and consumption of raw wool

Billion pounds



1988 preliminary. Clean content weight. Production data on a marketing basis.

Vegetables

U.S. vegetable production in 1989 should be greater than the 1988 level. Fresh vegetable exports were up 17 percent in 1988, reflecting larger shipments to Canada and Japan. Per capita fresh vegetable use reached 100 pounds for the first time due to higher lettuce and onion use. Consumption of fresh potatoes rose from 49 pounds per person in 1987 to 55 pounds in 1988.

Chart 255
Fresh and processing vegetable production

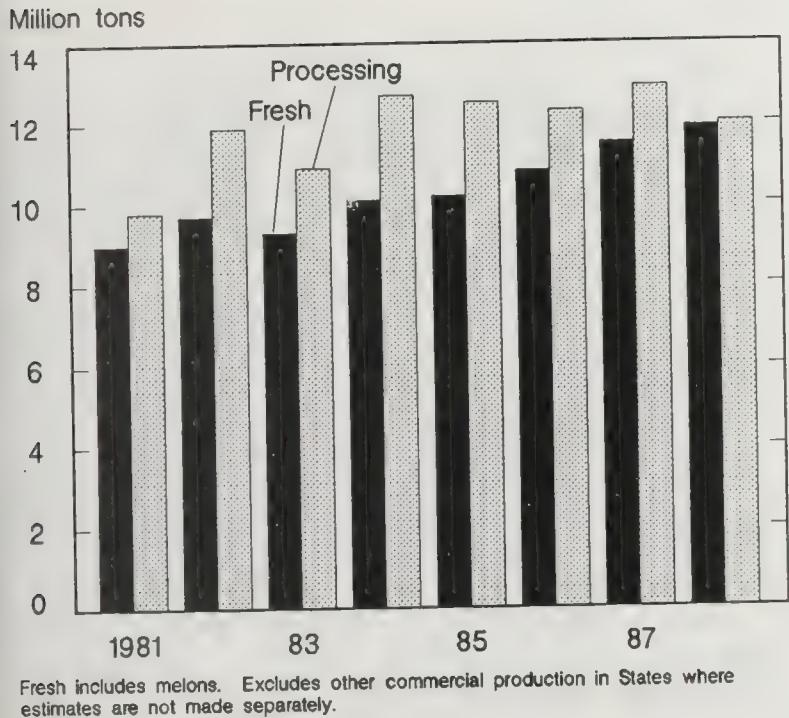


Chart 256
Destination of U.S. fresh vegetable exports

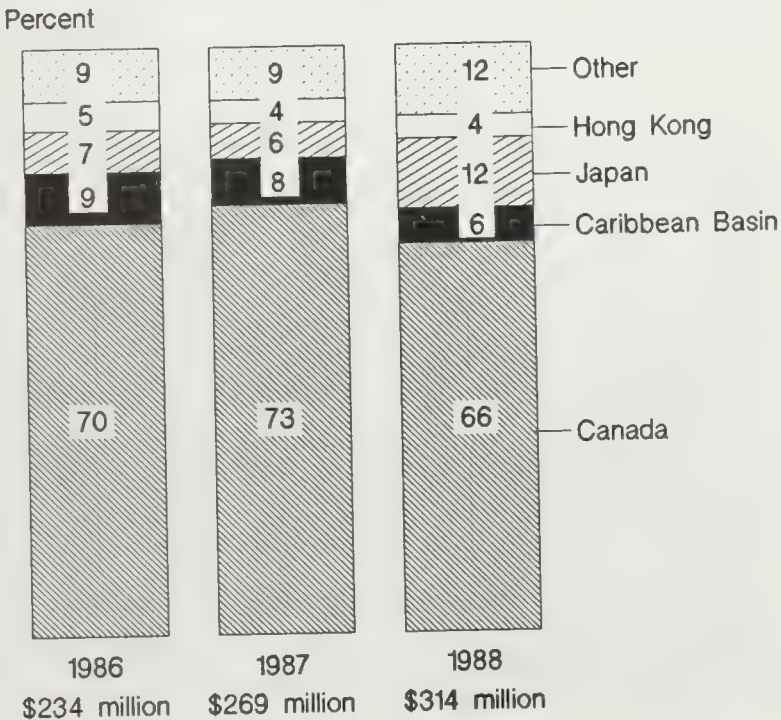


Chart 257
Per capita use of vegetables

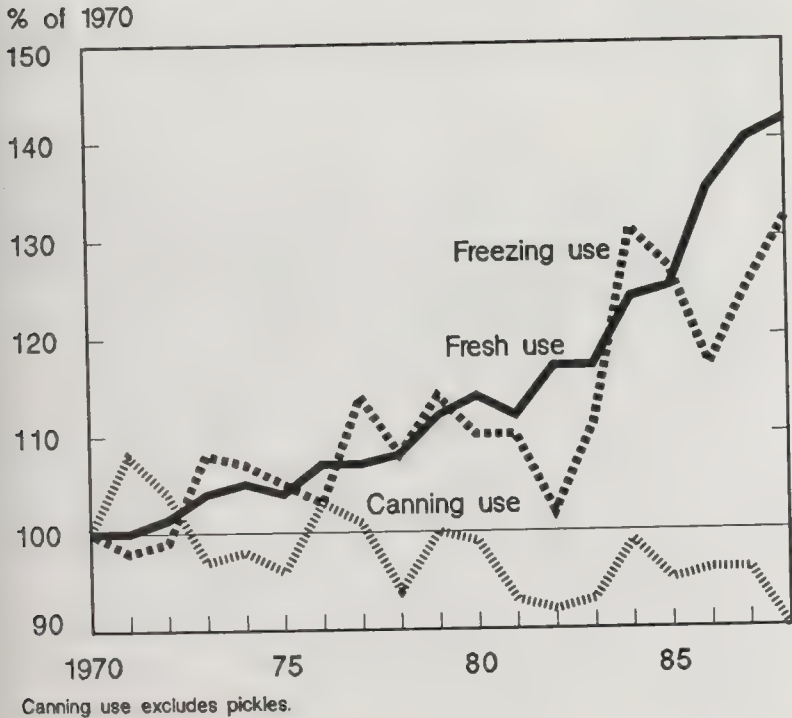
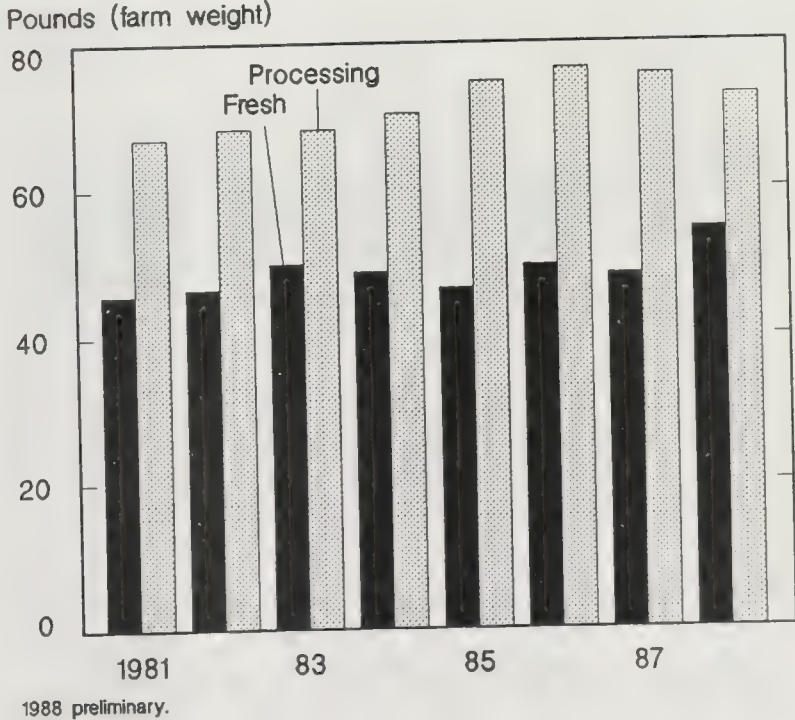


Chart 258
Per capita utilization of potatoes

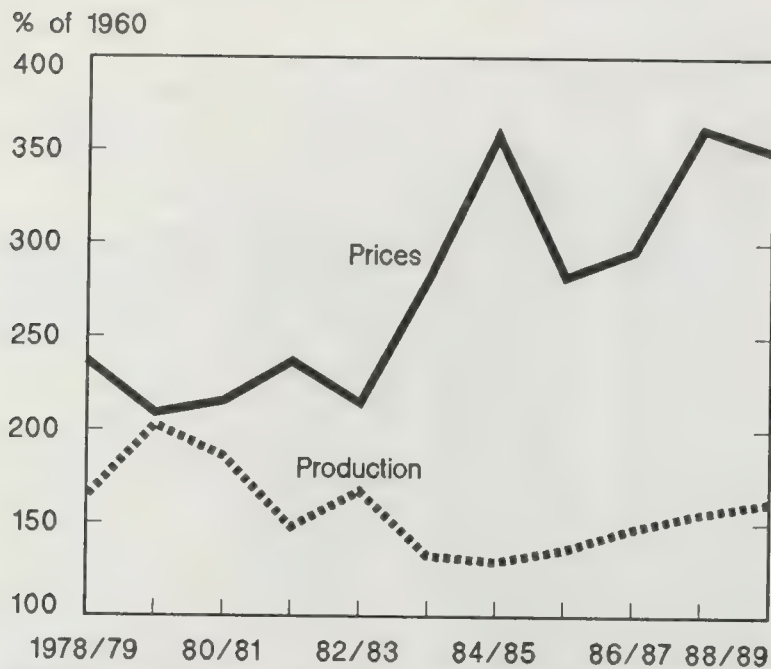


Fruit

Citrus fruit production in 1988/89 totaled 13.1 million short tons, up 4 percent from 1987/88. Per capita consumption of citrus fruit totaled 113.6 pounds in 1988, up 1 percent. Noncitrus fruit production was down 2 percent at 15.2 million short tons in 1988. Per capita consumption of noncitrus fruit totaled 97.7 pounds in 1988, down 5 percent.

Chart 259

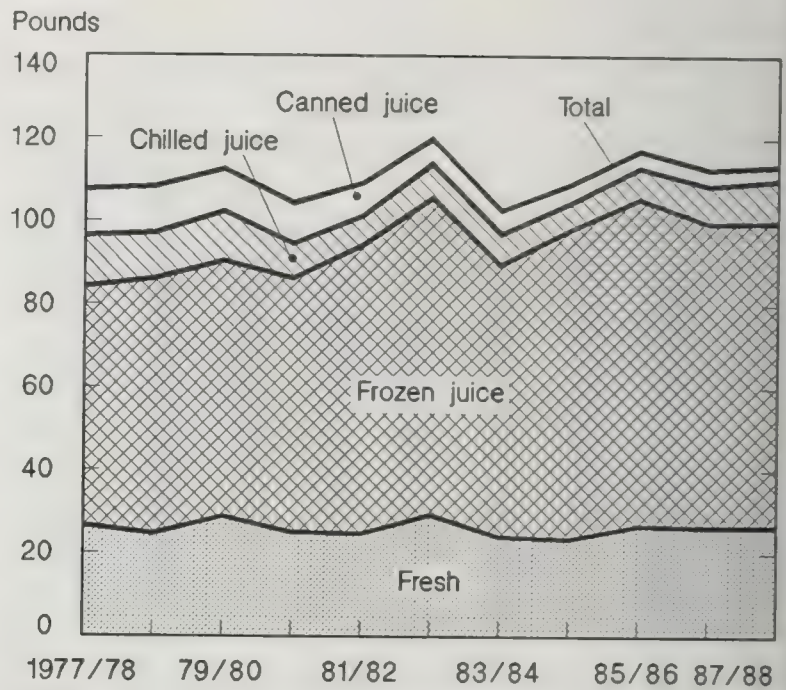
Citrus fruit production and farm prices



1988/89 preliminary. Production of all citrus fruits. Season average growers' prices weighted by production. Crop years.

Chart 260

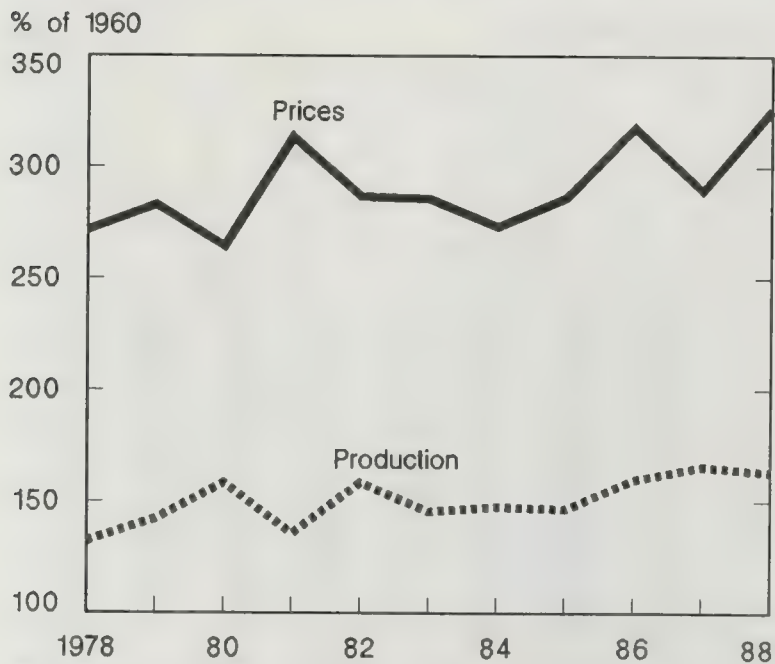
Per capita consumption of citrus fruit



1987/88 preliminary. Fresh-weight basis. Crop years.

Chart 261

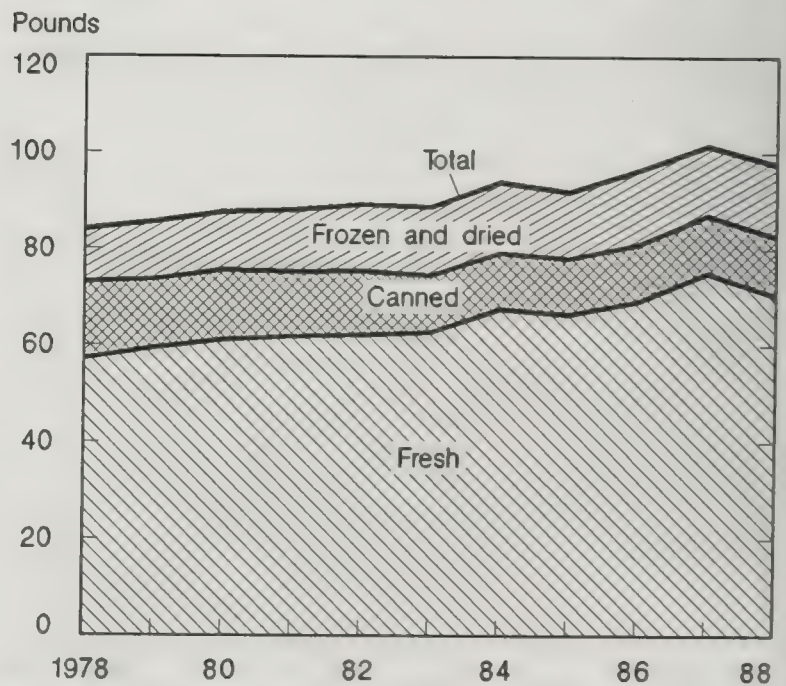
Noncitrus fruit production and farm prices



1988 preliminary. Production of 15 major fruits. Season average growers' price weighted by production.

Chart 262

Per capita consumption of noncitrus fruit



1988 preliminary. Fresh-equivalent basis. Canned includes fruit and juice.

Fruit and Tree Nuts

U.S. exports of fresh fruit increased 17 percent due to larger shipments to Japan, other Asian countries, Canada, and Europe. Bearing acreage of citrus and noncitrus fruits increased slightly in 1988, but tree nuts moderately declined. U.S. tree nut production dropped 6 percent. Tree nut exports rose nearly 18 percent, reflecting increased sales to Europe, Japan, and the Soviet Union.

Chart 263
Destination of U.S. fresh fruit exports

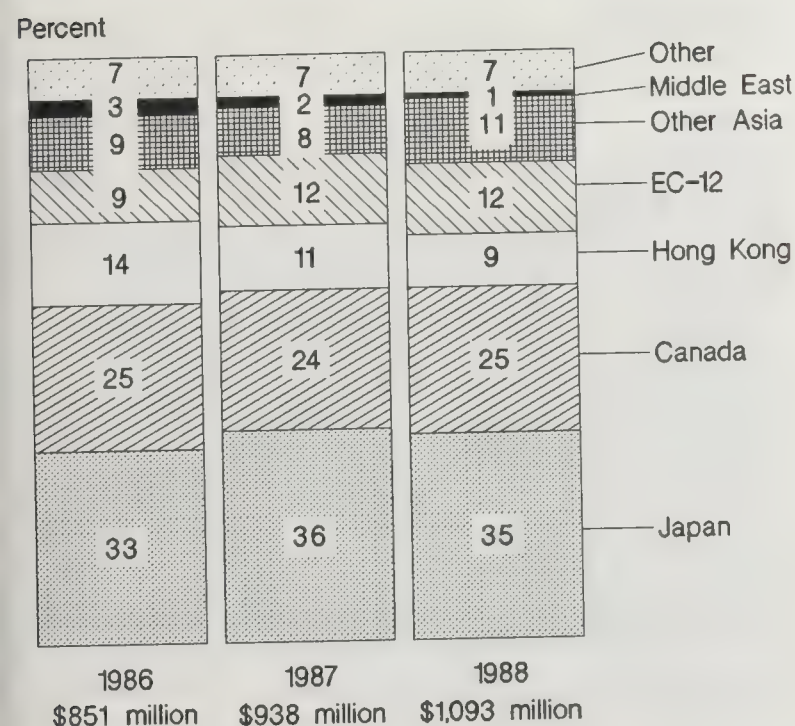


Chart 264
Fruit and tree nuts bearing acreage

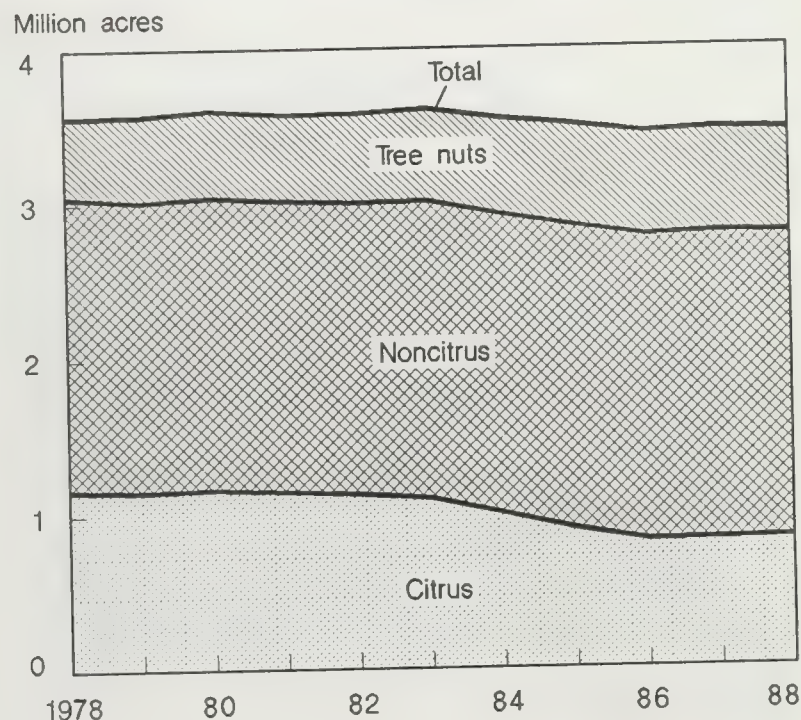


Chart 265
Tree nut production and value of production

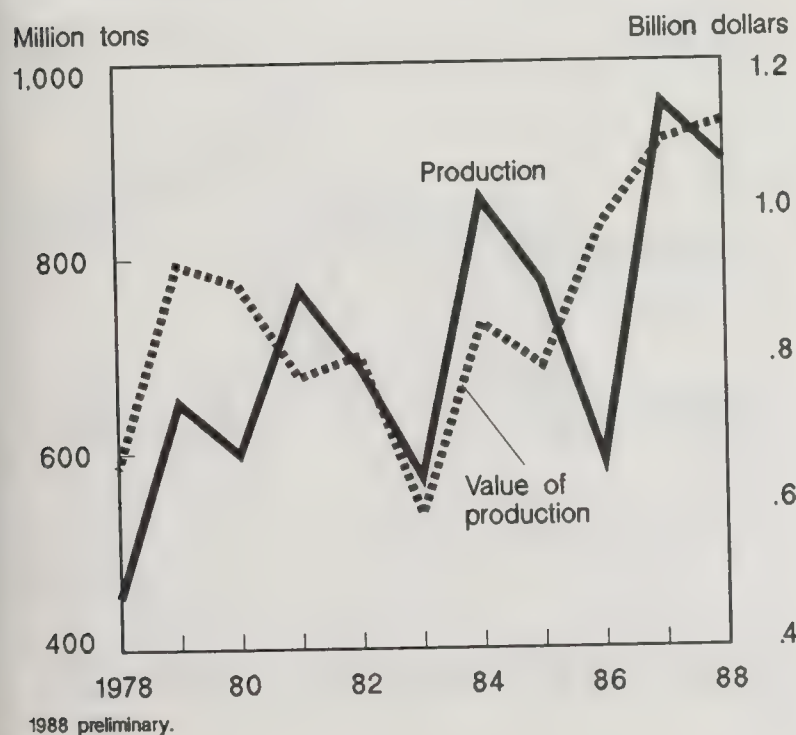
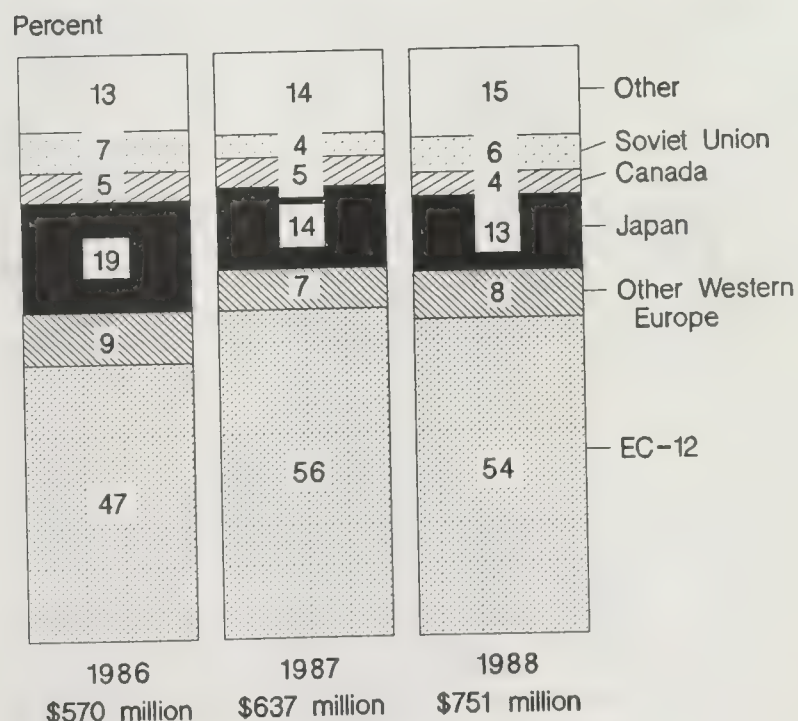


Chart 266
Destination of U.S. tree nut exports

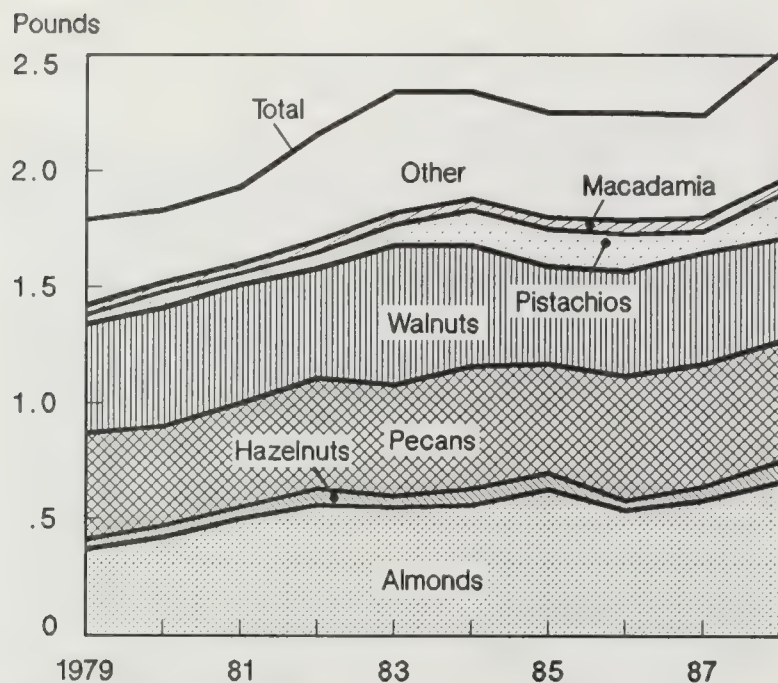


Tree Nuts and Tropical Products

Per capita consumption of tree nuts was boosted to a record 10.76 pounds due to lower prices. Bean prices for coffee and cocoa are expected to remain below those of previous years. U.S. consumption of coffee and cocoa, at best, may increase only slightly, while declines in retail prices will be limited.

Chart 267

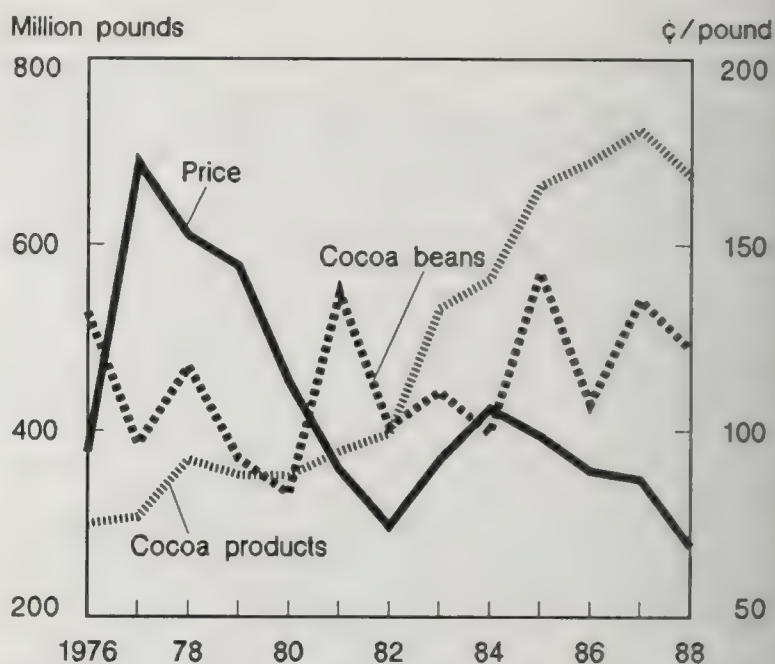
Per capita consumption of tree nuts



1988 preliminary. Shelled basis.

Chart 268

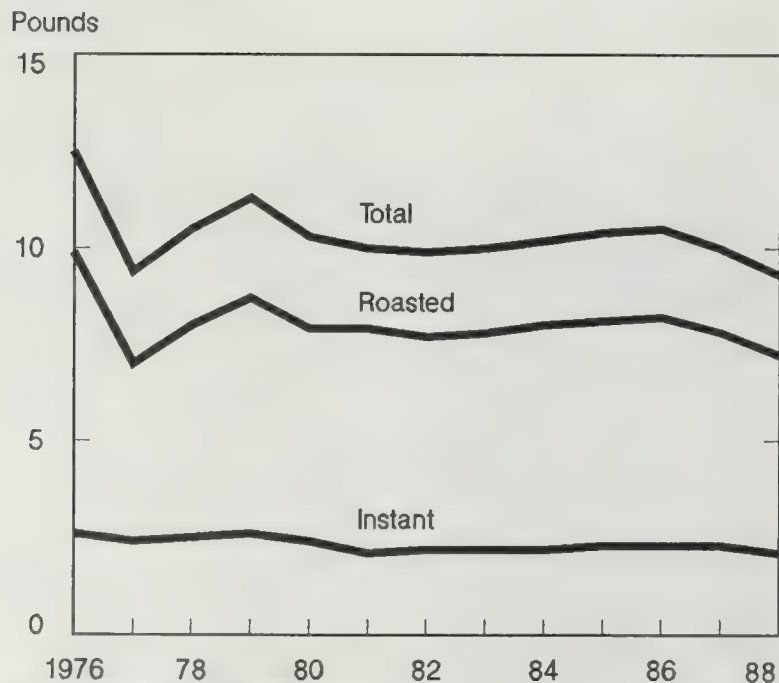
U.S. cocoa imports and prices



Price for cocoa beans is the average of nearest-three active futures trading months on the Coffee, Sugar, & Cocoa Exchange, Inc.

Chart 269

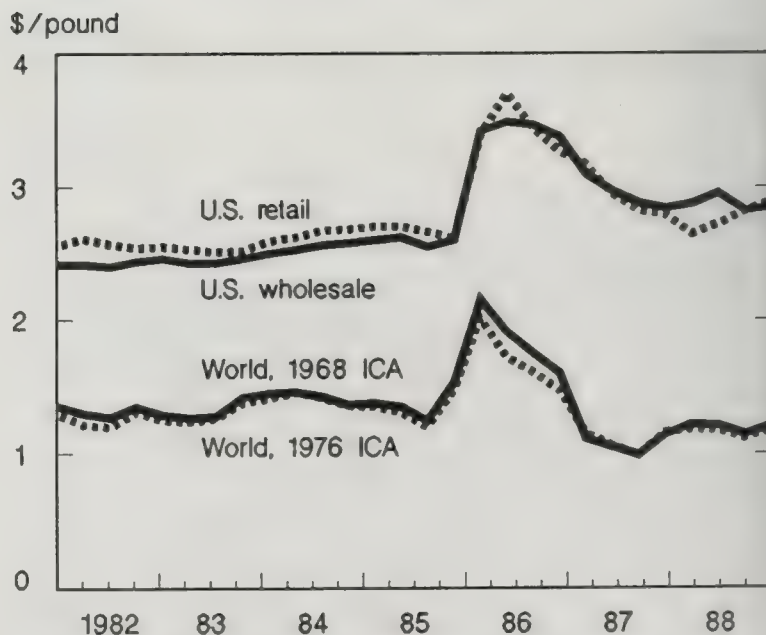
U.S. per capita consumption of coffee



1988 preliminary. Green bean equivalent.

Chart 270

World and U.S. coffee prices



Roasted for United States and green bean for world. ICA is International Coffee Agreement. 1976 ICA based on composite of other mild Arabica and Robusta coffees.

Sugar

U.S. beet sugar production fell in 1988 from the 1987 high. Domestic production accounted for almost 84 percent of total sources. Domestic sugar prices increased in 1988. Per capita use of corn sweeteners (including HFCS) exceeded sugar in 1987.

Chart 271
U.S. beet and cane sugar production

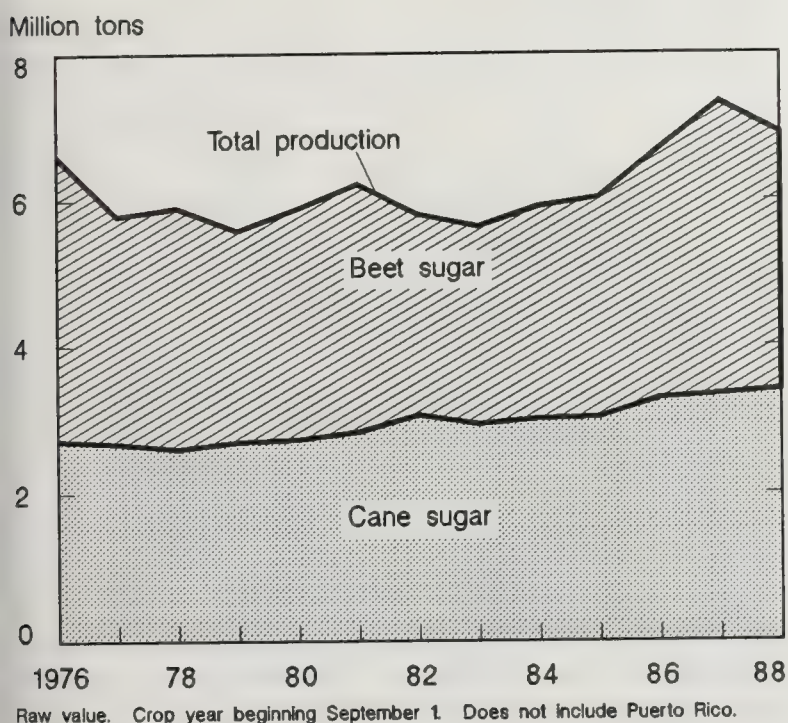


Chart 272
Sources of sugar used in the United States

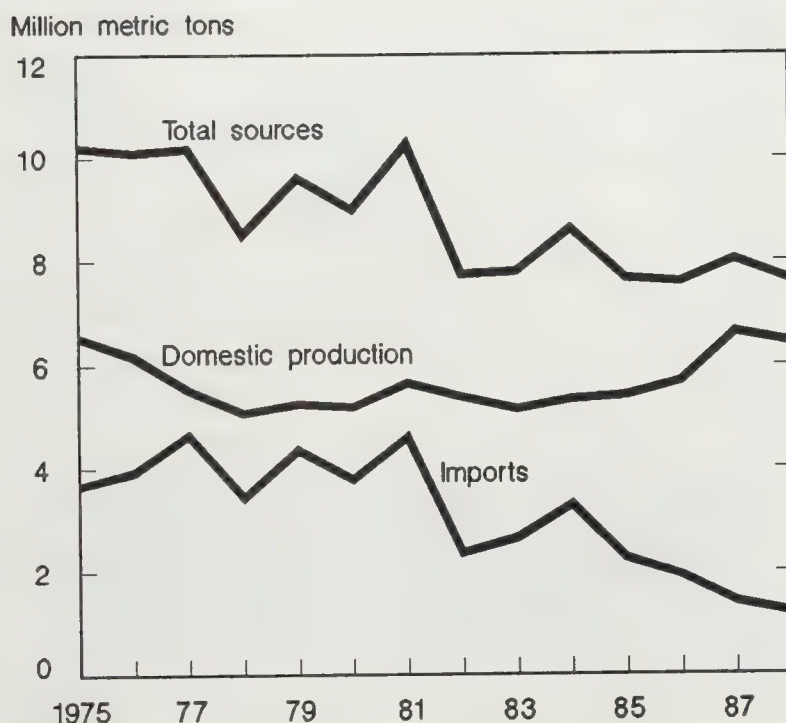


Chart 273
U.S. sugar prices

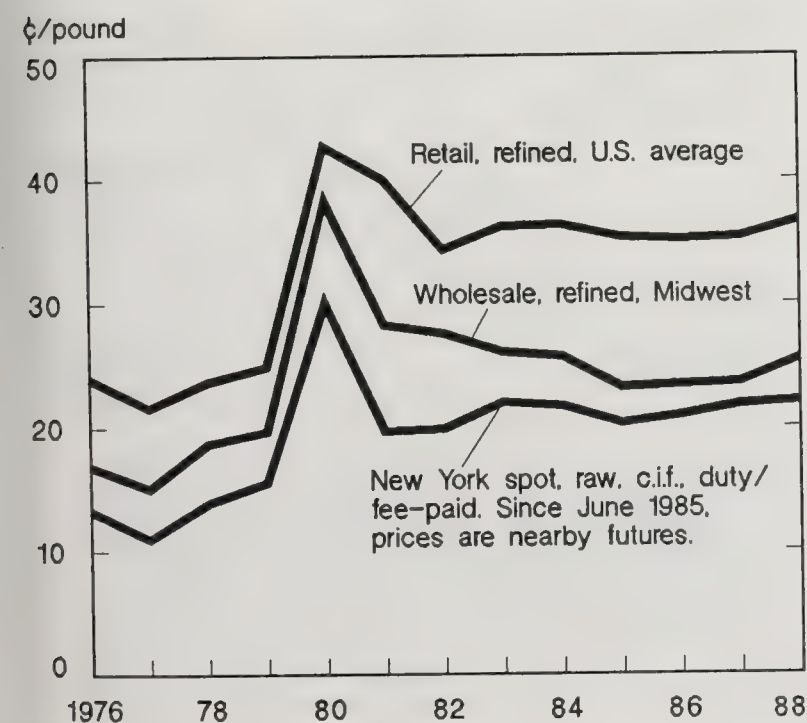
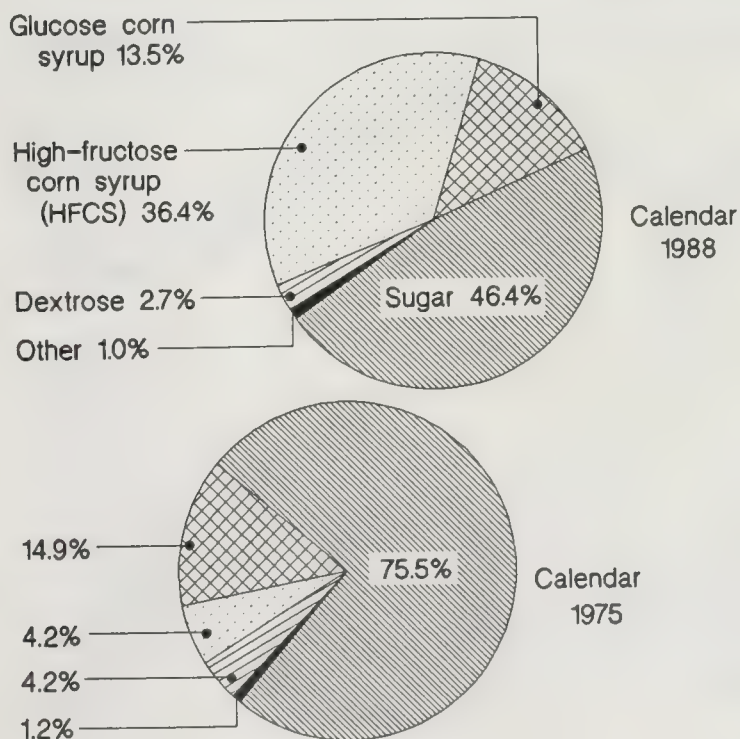


Chart 274
Per capita consumption of caloric sweeteners

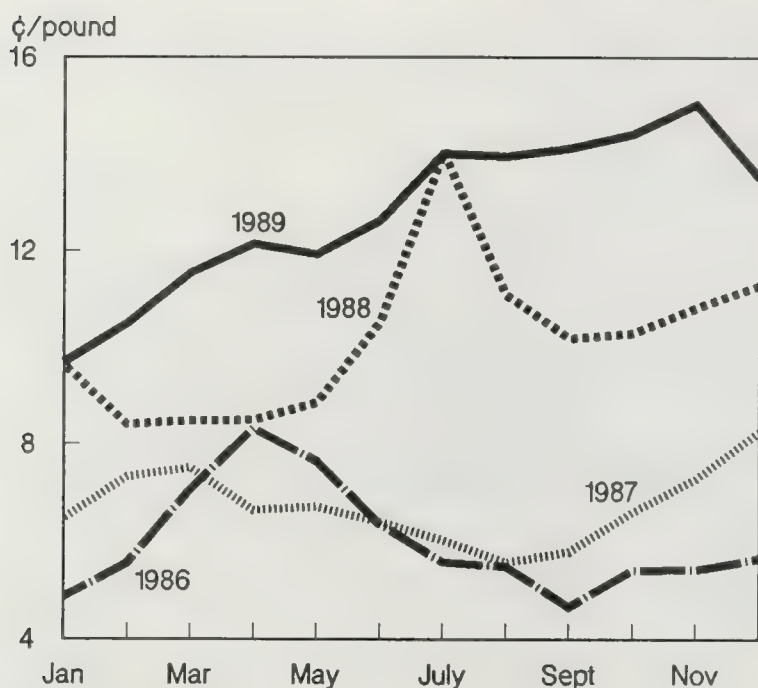


Sugar

World sugar prices have risen from 3.7 cents per pound in 1985/86 to 11.6 cents per pound in 1988/89. Global consumption rose from 93.2 million metric tons in 1981/82 to 108.7 million metric tons in 1989/90. Ending stocks dropped to about 18 percent of estimated consumption in 1989/90. The EC is the world's largest sugar producer and exporter.

Chart 275

World price for raw sugar



No. 11, f.o.b. Caribbean.

Chart 276

World sugar production and consumption

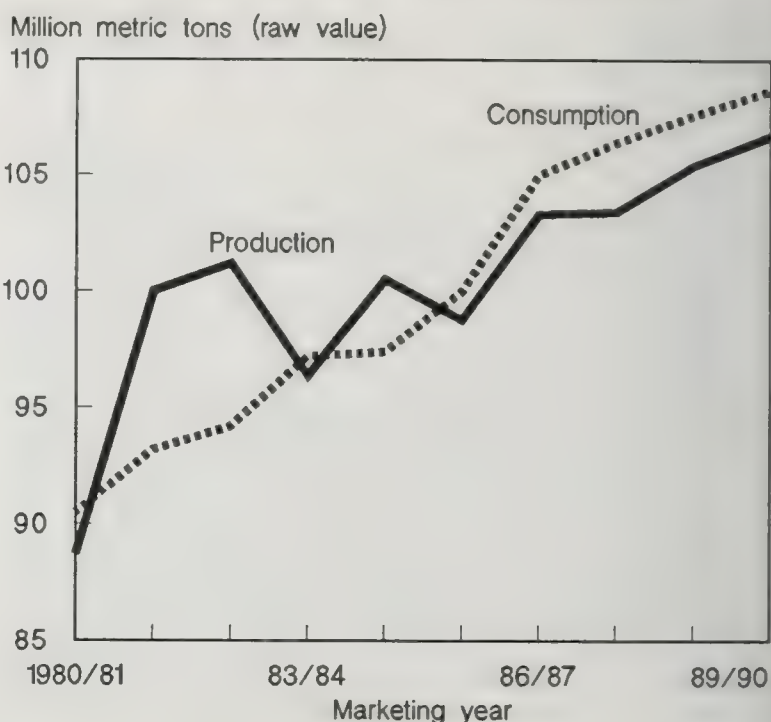


Chart 277

World sugar ending stocks and world sugar prices

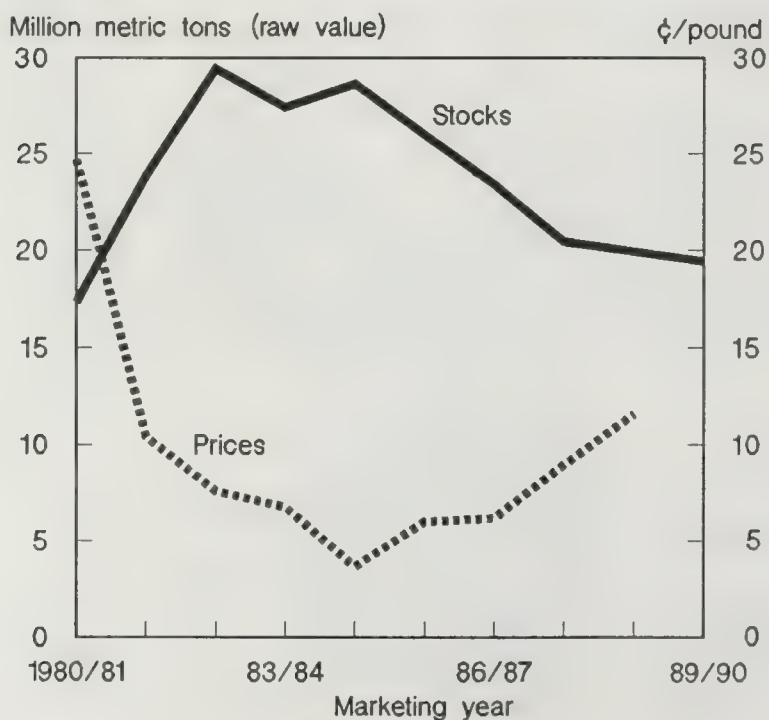
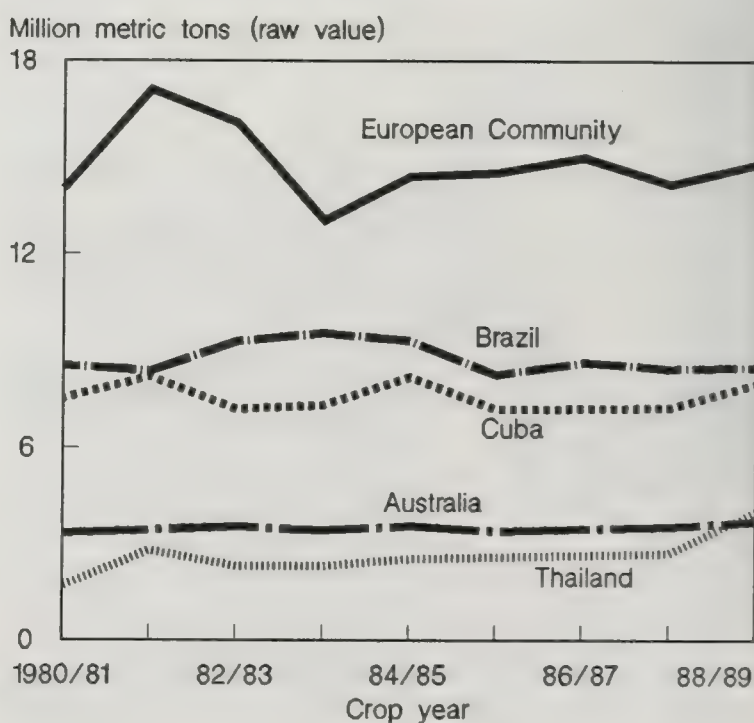


Chart 278

Sugar production: Major exporters



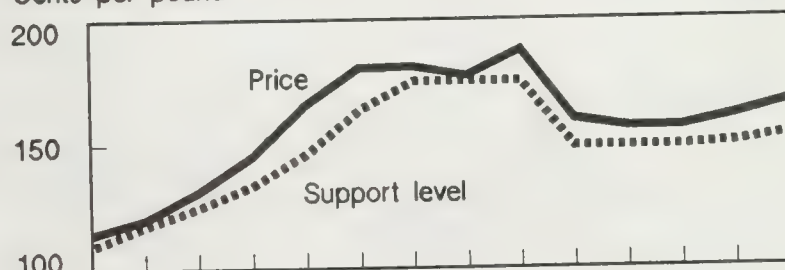
Tobacco

Total 1989 U.S. tobacco production, including burley, flue-cured, and all other kinds, was about 1.48 billion pounds, up about 8 percent from the 1988 crop. Burley price supports averaged \$1.532 per pound in 1989 and flue-cured supports averaged \$1.468. Burley and flue-cured supports will both increase in 1990.

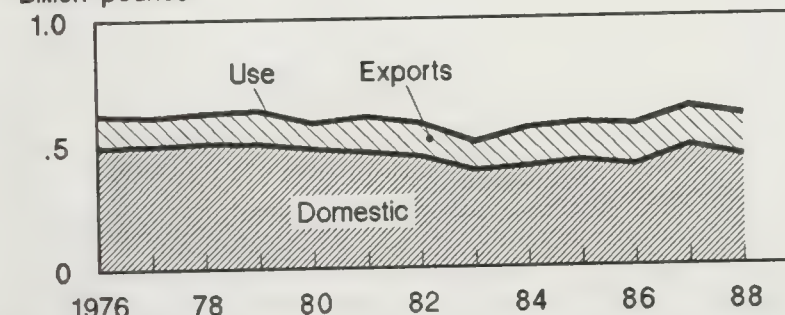
Chart 279
Burley tobacco: Supply, price, use

Billion pounds
2.5
2.0
1.5
1.0
0.5
0

Cents per pound
200
150
100



Billion pounds
1.0
0.5
0



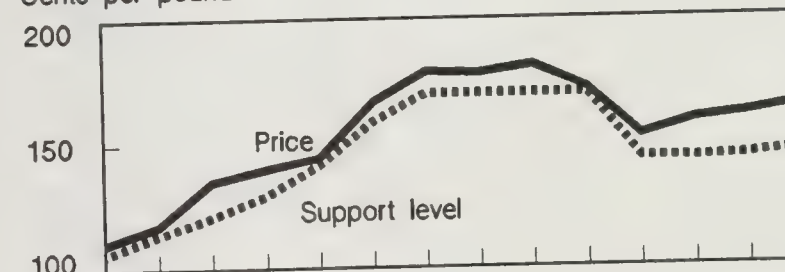
1988 preliminary, 1989 forecast. Trade stocks include manufacturers' and dealers'.

Crop year beginning October 1.

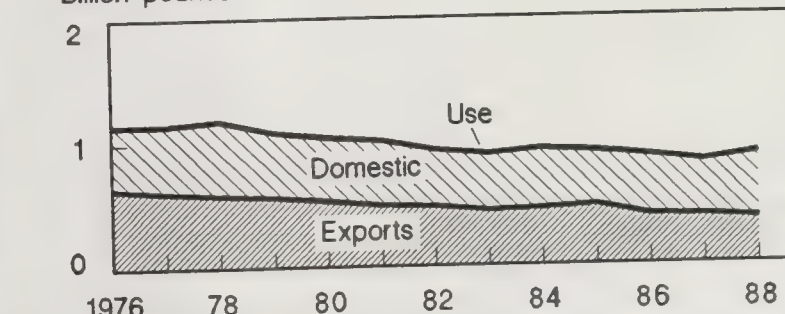
Chart 280
Flue-cured tobacco: Supply, price, use

Billion pounds
4
3
2
1
0

Cents per pound
200
150
100



Billion pounds
2
1
0



1988 preliminary, 1989 forecast. Trade stocks include manufacturers' and dealers'.

Crop year beginning July 1.

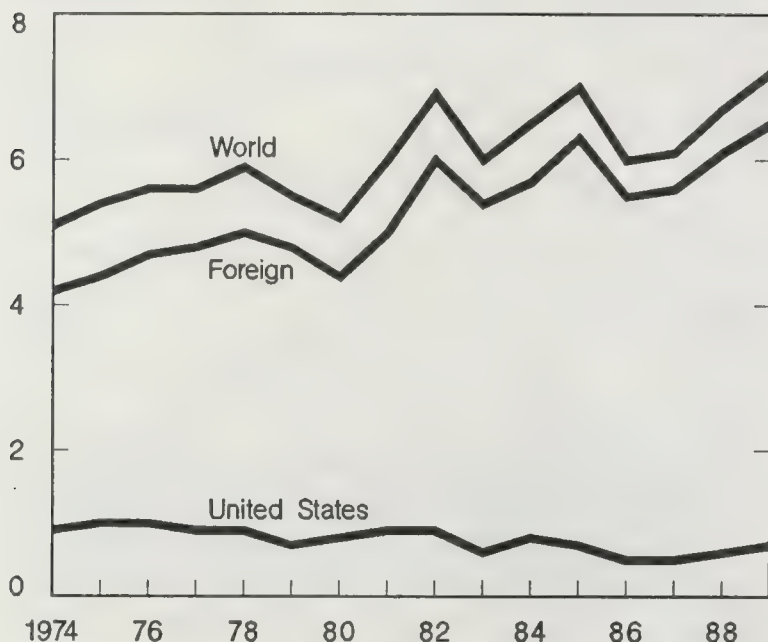
Tobacco

Total 1988 world tobacco production was estimated at 7.2 million tons, 7 percent above last year's harvest. Both cigarette production and tobacco use fell during 1980-86 before rebounding in 1987 and 1988. Domestic consumption continues to fall.

Chart 281

Unmanufactured tobacco production

Million metric tons

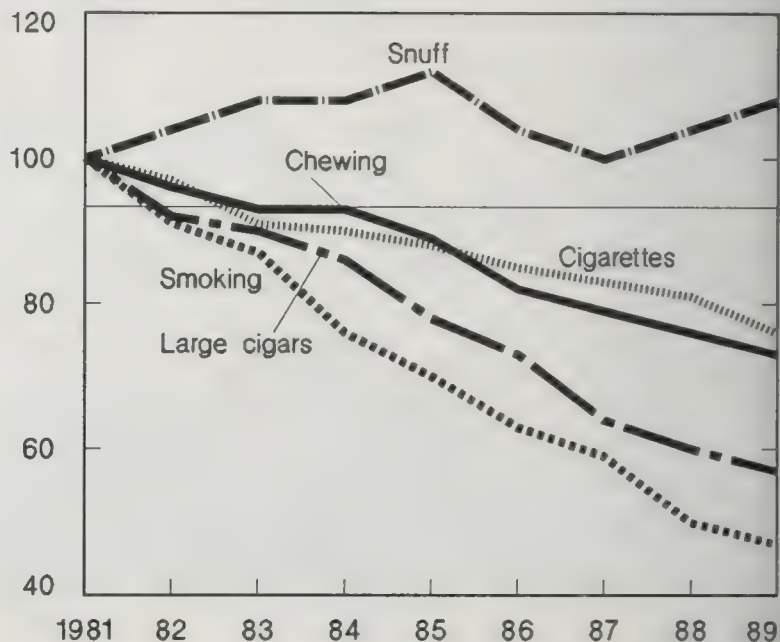


1988 revised, 1989 forecast.

Chart 282

Per capita consumption of tobacco products

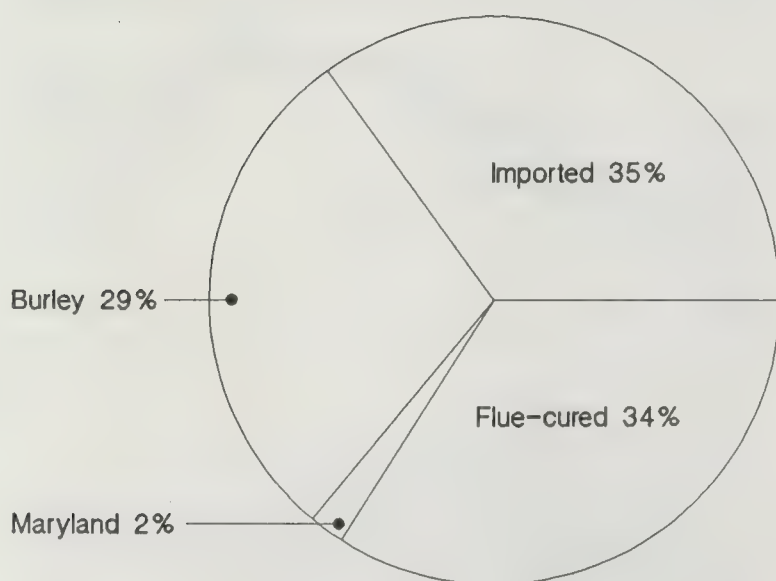
% of 1981



1989 preliminary. Persons 18 years and older.

Chart 283

Tobacco use in cigarettes



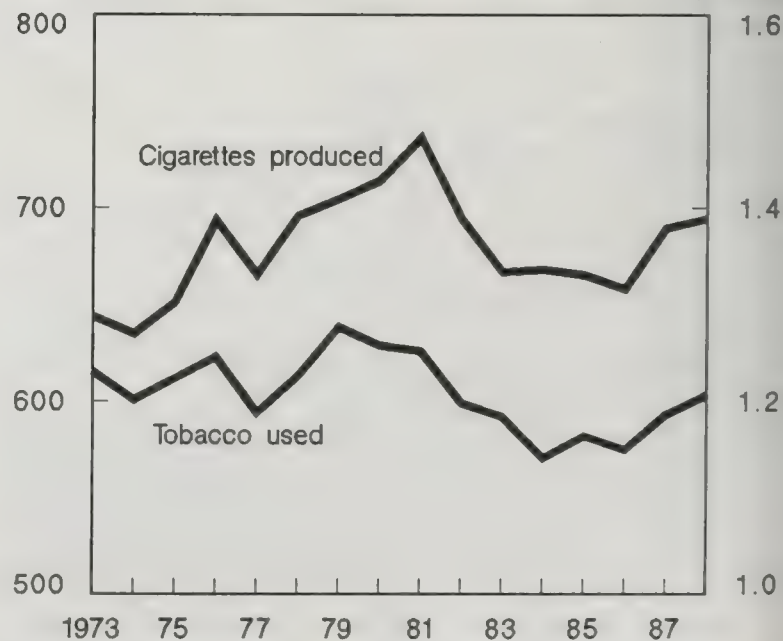
1986-88 average.

Chart 284

Cigarettes produced and tobacco used

Billion cigarettes

Billion pounds



Billion pounds in unstemmed processing weight.

Transportation

The increased volume of international grain trade and reductions in excess shipping capacity caused ocean rates to rise in 1987 and 1988. The rise in rail rates in 1988 is due more to a rise in rail freight volume than to a rise in costs. Increased grain exports carried barge shipments and rates upward.

Chart 285
Ocean freight rates from U.S. gulf

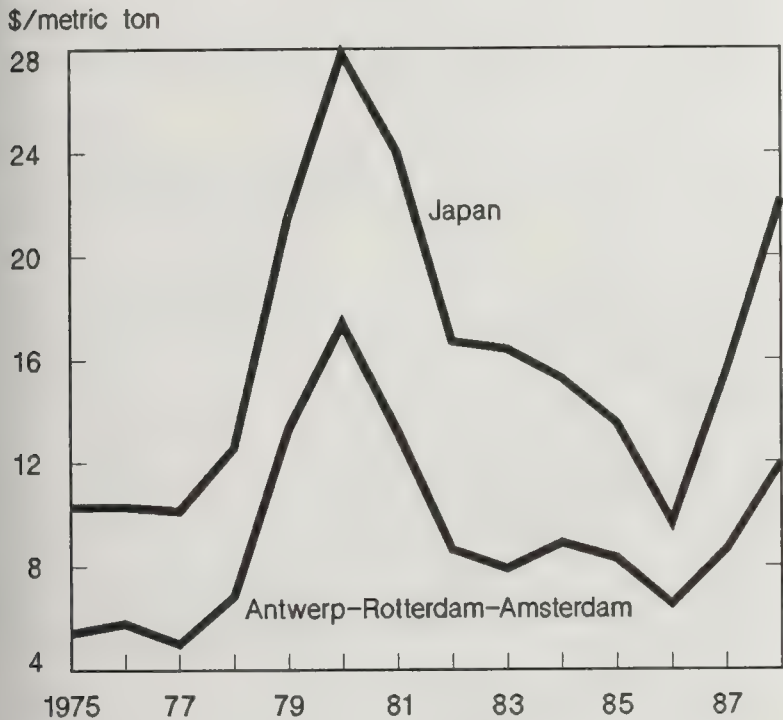


Chart 286
Rail freight rates for agricultural products

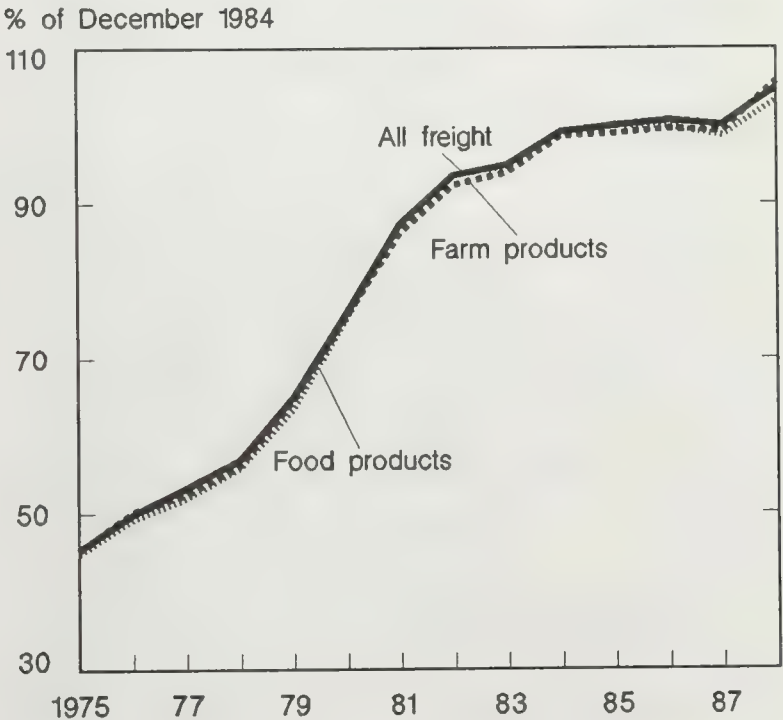


Chart 287
Spot barge rates for grain

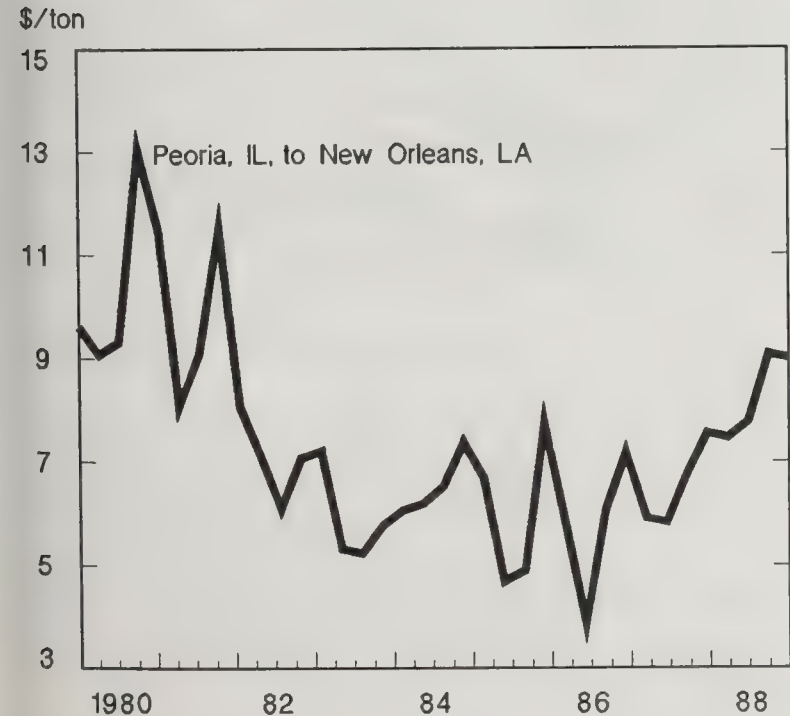
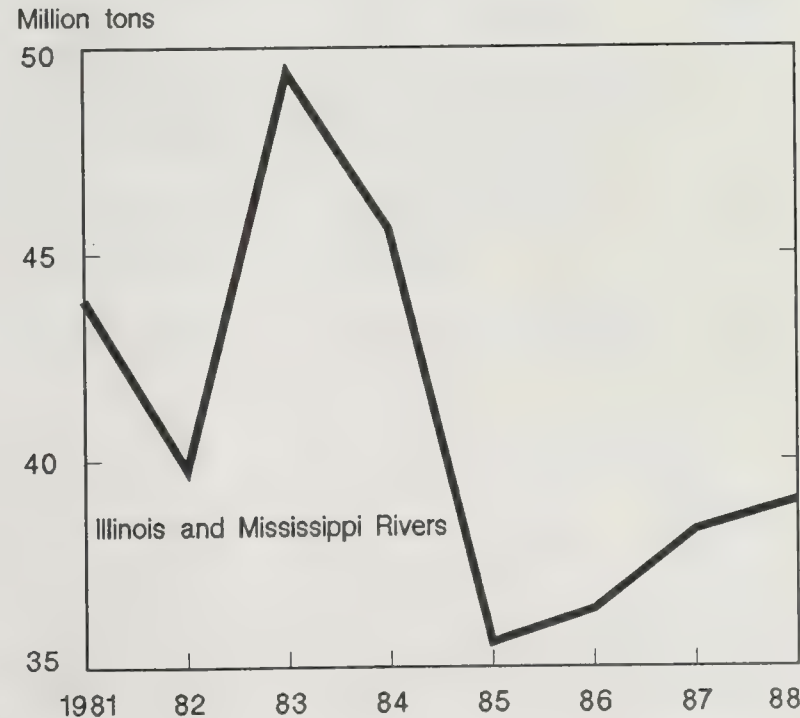


Chart 288
Barge shipments of grain



Transportation

Increases in rail loadings of grain since 1985 resulted chiefly from increased deliveries to Gulf Coast ports. Trucks dominate fresh produce distribution due to superior services such as shorter delivery time, more delivery destinations, and better condition of produce on arrival. Rising interest and insurance costs outweighed declining fuel prices for trucks in 1988.

Chart 289

Carloads of grain shipped by rail

Million cars

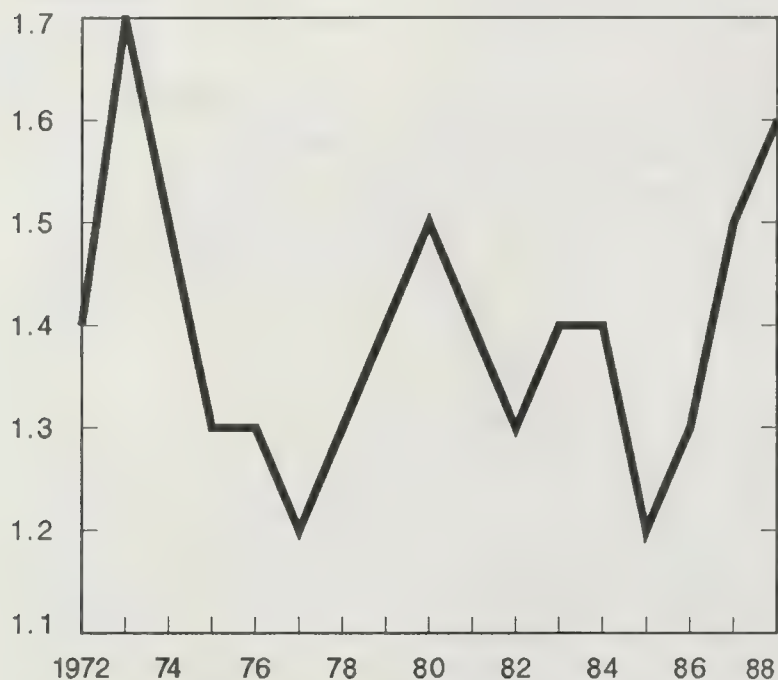


Chart 290

Fresh fruits and vegetables shipped by truck, rail, and piggyback

Million cwt

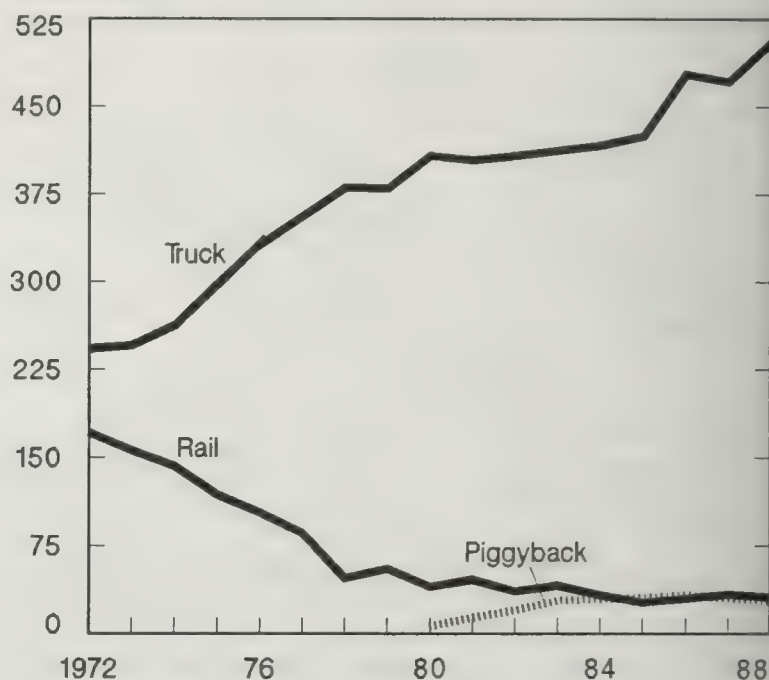


Chart 291

Costs of hauling fresh produce by truck

¢/mile

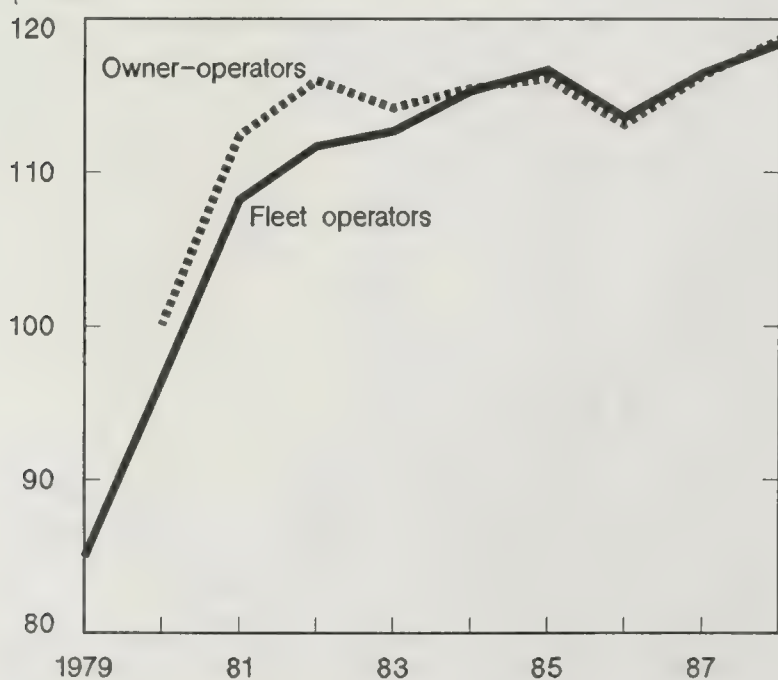
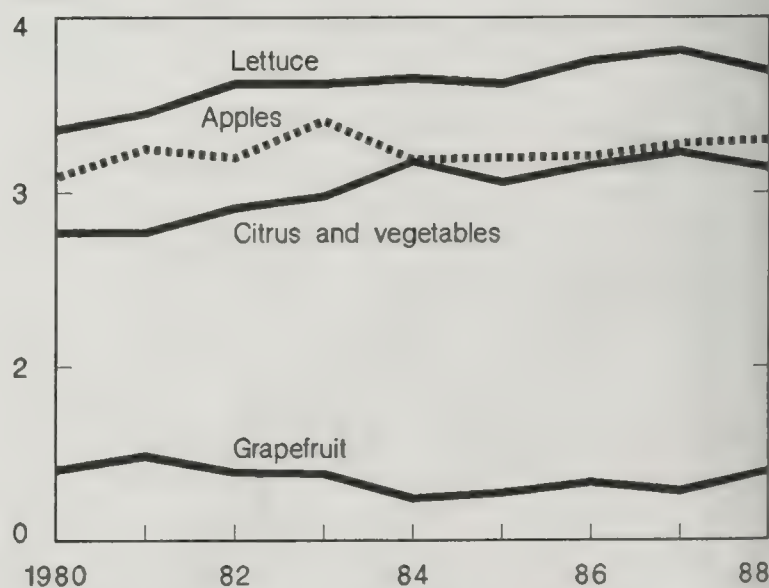


Chart 292

Truck rates for fresh produce

\$/box



Grapefruit rates from Florida to New York City. All other produce from West Coast to New York City. Source: Fresh Fruit and Vegetable Market News Service, AMS, USDA.

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Abstract

Shimanuki, Hachiro, and David A. Knox. 1991. Diagnosis of Honey Bee Diseases. U.S. Department of Agriculture, Agriculture Handbook No. AH-690, 53 p.

Apiary inspectors and beekeepers must be able to recognize bee diseases and parasites and to differentiate the serious diseases from the less important ones. This handbook describes laboratory techniques used to diagnose diseases and other abnormalities of the honey bee and to identify parasites and pests of the honey bee. Emphasis is placed on the techniques used by the U.S. Department of Agriculture Bee Research Laboratory. Included are directions for submitting, through APHIS-PPQ or State regulators, samples of suspected Africanized honey bees for identification of subspecies. Also included are directions for sending diseased brood and adult honey bees for diagnosis of bee disease.

Keywords: honey bee disease, honey bee disorder, honey bee parasite, honey bee pest, Africanized honey bee

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This publication supersedes "Diagnosis of Honey Bee Diseases, Parasites, and Pests," ARS-NE-87.

Issued April 1991



Diagnosis of Honey Bee Diseases

Hachiro Shimanuki¹ and David A. Knox

Introduction

Inspection for bee disease is an important part of beekeeping. Apiary inspectors and beekeepers must be able to recognize bee diseases and parasites and to differentiate the serious diseases from the less important ones. The purpose of this publication is to acquaint readers with laboratory techniques used to diagnose diseases and to detect and identify parasites, pests, and other abnormalities of the honey bee. We realize that different laboratory methods are used by others; where possible, those methods are described. However, emphasis is placed on the techniques used by the U.S. Department of Agriculture Bee Research Laboratory. Directions for submitting samples for diagnosis or subspecies identification are included in appendixes A and B.

Methods of Diagnosing Disease

Techniques of Microscopic Examination


Most bee diseases can be diagnosed by observing the associated microorganisms with a light microscope. The following techniques are commonly used to prepare microscope slides for examination:

Modified Hanging Drop

The modified hanging drop technique (Michael 1957) can be very useful for differentiating diseases of the brood. Residue from a suspected cell is first mixed with water. Then a drop of this suspension (smear) is placed on a cover glass. The suspension used should always be dilute and only slightly turbid. The smear is dried and fixed under a heat lamp, or the smear can be air dried and heat fixed by passing it rapidly through a bunsen burner flame two or three times. The fixed smear is stained with carbol fuchsin² or a suitable spore stain for 10 seconds. Enough stain should be placed on the cover glass to cover the entire smear. The excess

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²Solution A: 0.3 g basic fuchsin (90% dye content), 10 mL ethyl alcohol (95%); solution B: 5 g phenol, 95 mL distilled water. Mix solutions A and B.



stain is then washed off with water. While the smear is still wet, the cover glass is inverted with the smear side down and placed onto a standard microscope slide previously coated with a very thin layer of immersion oil. The slide is gently blotted dry and examined with a microscope using the oil immersion objective. Results: Organisms that are not heat fixed are caught in areas where pockets of water have formed in the oil, and the organisms usually exhibit Brownian movement (see section on American foulbrood).

Simple Stain

This method relies solely on differentiating the bacteria by morphology. Place a drop of the suspension directly on a microscope slide. Heat fix and stain the smear as described in the previous section. Carbol fuchsin, methylene blue, and safranin are examples of stains that can be used. Air-dry or gently blot the stained smear. Place a drop of immersion oil directly on the smear. No cover glass is necessary. Examine the slide, using the oil immersion objective. Results: Organisms are uniformly stained and easily distinguished.

Gram Stain

The Gram stain is a standard microbiological method that can be substituted for the simple stain. Briefly, the procedure is as follows: A fixed smear is stained with crystal violet, immersed in iodine solution, decolorized in ethyl alcohol, and counterstained with safranin. Results: Gram-positive organisms are blue; Gram-negative organisms are red.

Wet Mount

The wet mount is especially useful for examining fungi or protozoa. Macerate a portion of the sample in water. Place a drop of the suspension on a microscope slide, and carefully drop the cover glass on it to minimize air pockets. No stain is required. The wet mount is usually examined with the dry objectives of a microscope. Results: Organisms refract light and are therefore visible on the slide. A phase-contrast microscope may be helpful, especially if an oil immersion objective is required.

Microinjection Techniques

To diagnose some diseases or to determine toxic levels of sample materials, it may be necessary to feed or inoculate larvae, pupae, or adult honey bees. Michael (1960) developed a technique using a microinjector

equipped with a syringe and a 30-gauge needle. The microinjector can be calibrated to repeatedly deliver uniform inoculating volumes as small as 1 μ L. The apparatus can be used to introduce material orally into the midgut (ventriculus) of a larva or to feed individual adult honey bees. The microinjection technique can also be adapted to direct injections into the body cavity of larvae, pupae, and adults.

Collecting Honey Bee Larvae and Pupae

Honey bee larvae 3 to 5 days old are readily obtained by removing a brood frame containing the desired larvae from a colony and placing it horizontally above a towel-lined tray in an incubator at 34°C. Within a few hours, the larvae crawl from their cells and drop to the tray below. Pupae can be easily obtained by collecting 5-day-old larvae as described above and incubating them in petri dishes until pupation occurs. This method of collecting larvae and pupae in large numbers saves considerable time and labor. It also eliminates the damage that can occur when attempting to remove these immature forms from cells by mechanical means.

Oral Introduction

Larvae

Honey bee larvae as young as 3 days and weighing as little as 25 mg can be force-fed by carefully inserting the needle through the mouthparts and into the esophagus (fig. 1). When the actuating lever is depressed, a

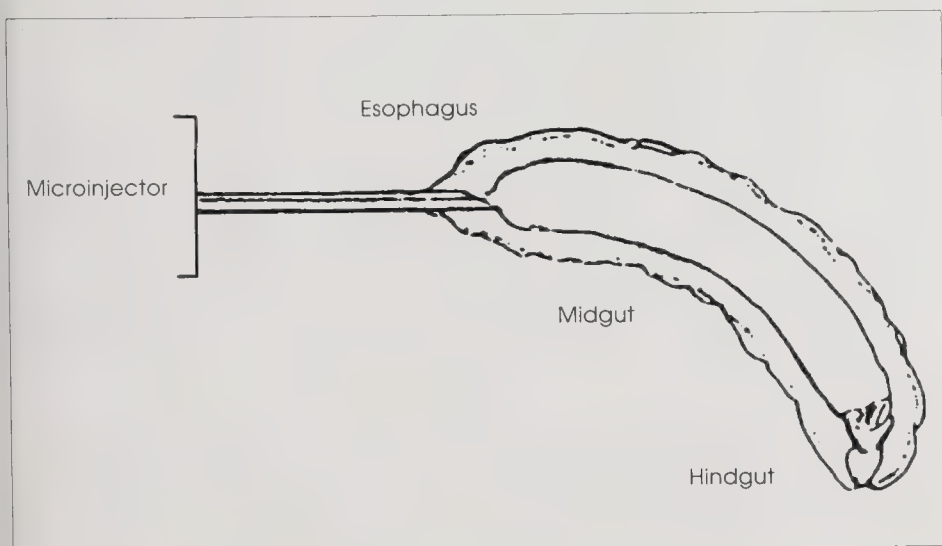



Figure 1. Force-feeding a honey bee larva.



predetermined volume of material is propelled through the esophagus and into the midgut, with no physical damage to the larva. After feeding, the larvae are placed in petri dishes lined with filter paper and incubated at 34°C.

Adults

Individual adult honey bees can also be fed known volumes using the microinjector. Adult bees are collected and held in a cage for about 4 hours without food. The material to be fed, at the final concentration, should be mixed into a sucrose solution to make it attractive to the bees. The microinjector is first actuated to produce a known volume of liquid at the tip of the needle. Then a bee from the cage is grasped by the wings, held up to the drop of liquid, and allowed to feed. Cold temperatures can be used to slow the bees and make them easier to handle. Avoid the use of carbon dioxide as an anesthetic to aid in handling bees, because they are reluctant to feed after exposure to carbon dioxide and their longevity is reduced. After feeding, the bees are placed in small cages with a supply of sugar syrup and held in an incubator at 34°C.

Direct Injection

Care should be taken to insert only the tip of the needle into the hemocoel and to not exceed inoculating volumes of 2 μ L per bee.

Brood

Injections are usually confined to 4- to 5-day larvae. The larva is held gently between the first and second fingers and the thumb, and the larva must be absolutely parallel to the needle. After the integument is punctured by the needle under gentle pressure, the inoculum is expelled directly into the dorsal blood vessel; the needle is then withdrawn in a slow, steady movement. Any excessive pressure on the larva by the fingers, particularly when withdrawing the needle, must be avoided to prevent bleeding. Pupae can be inoculated dorsally between the third and fourth abdominal segments or through the propodeum of the thorax. After injection, the larvae or pupae are placed in petri dishes lined with filter paper and incubated at 34°C. If excessive bleeding has occurred, it can be seen on the filter paper.

Pupae can also be left in brood combs and inoculated in the head capsule (Wilson 1970). The pupal head is exposed by removing the cell cap, and the needle is inserted between the ocelli or through the clypeal sclerite.



Adults

Adult bees can be injected either through the propodeum of the thorax or dorsally through the intersegmental membrane between the third and fourth abdominal segments. Adult bees should be carefully subjected to carbon dioxide anesthetic before and during the process of injection. When bee longevity is a factor in the test, cold temperature can be used as an anesthetic. After injection, the bees are placed in small cages with a supply of sugar syrup and held in an incubator at 34°C.

Removal of Digestive Tract

Intact digestive tracts that have been removed from adult honey bees are very useful for the detection of protozoan diseases (refer to fig. 9). The digestive tracts can be easily obtained by removing the head of the bee to free the digestive tract, grasping as much of the stinger as possible with a pair of fine tweezers, and then with a steady, gentle pull withdrawing the entire digestive tract. Freshly killed honey bees are required for this procedure.

Brood Diseases

Brood combs from healthy colonies typically have a solid and compact brood pattern. Almost every cell from the center of the comb outward contains an egg, larva, or pupa. The cappings are uniform in color and are convex (higher in center than at margins). The unfinished cappings of healthy brood may appear to have punctures, but since cells are always capped from the outer edges to the middle, the holes are always centered and have smooth edges. In contrast, brood combs from diseased colonies usually have a spotty brood pattern (pepperbox appearance), and the cappings tend to be darker, concave (sunken), and punctured. Also, the combs may contain the dried remains of larvae or pupae (scales), which are found lying lengthwise on the bottom side of brood cells. Sometimes scales are difficult to locate because of the condition of the comb. Scale material can be easily located using long-wave ultraviolet or near-ultraviolet light. Exposure to wavelengths of 3100-4000 angstroms will cause scale material to fluoresce. Some discretion must be used with this technique because honey and pollen may also fluoresce. Symptoms of various brood diseases are summarized in table 1.

Symptoms of a contagious disease are sometimes mimicked because of an unrelated factor. For instance, often brood that is neglected because of a shortage of nurse bees will die from either chilling or starvation.

Table 1. Comparative symptoms of various brood diseases of honey bees

Symptom	American foulbrood	European foulbrood	Sacbrood	Chalkbrood
Appearance of brood comb	Sealed brood. Discolored, sunken, or punctured cappings.	Unsealed brood. Some sealed brood in advanced cases with discolored, sunken, or punctured cappings.	Sealed brood. Scattered cells with punctured cappings, often with two holes.	Sealed and unsealed brood. Affected larvae usually on outer fringes.
Age of dead brood	Usually older sealed larvae or young pupae. ¹ Upright in cells.	Usually young unsealed larvae; occasionally older sealed larvae. Typically in coiled stage.	Usually older sealed larvae; occasionally young unsealed larvae. Upright in cells.	Usually older larvae. Upright in cells.
Color of dead brood	Dull white, becoming light brown, coffee brown to dark brown, or almost black.	Dull white, becoming yellowish white to brown, dark brown, or almost black.	Grayish or straw-colored, becoming brown, grayish black, or black. Head end darker.	Chalk white. Sometimes mottled with black spots.
Consistency of dead brood	Soft, becoming sticky to ropy.	Watery; rarely sticky or ropy. Granular.	Watery and granular; tough skin forms a sac.	Watery to pastelike.
Odor of dead brood	Slight to pronounced glue odor to gluepot odor.	Slightly sour to penetratingly sour.	None to slightly sour.	Slight, non-objectionable.
Scale characteristics	Uniformly lies flat on lower side of cell. Adheres tightly to cell wall. Fine, threadlike tongue of dead pupae may be present. Head lies flat. Brittle. Black.	Usually twisted in cell. Does not adhere tightly to cell wall. Rubbery. Black.	Head prominently curled toward center of cell. Does not adhere tightly to cell wall. Rough texture. Brittle. Black.	Does not adhere to cell wall. Brittle. Chalky white, mottled, or even black.

Symptoms can also be the result of a failing queen, laying workers, toxic chemicals, or poisonous plants. (See section on Noninfectious Diseases.)

Bacterial Diseases

American Foulbrood

Bacillus larvae is the bacterium that causes American foulbrood disease (AFB). *Bacillus larvae* is a slender rod with slightly rounded ends and a tendency to grow in chains (fig. 2). The rod varies greatly in length, from about 2.5 to 5 microns (μm), and is about 0.5 μm wide. The spore is oval and approximately twice as long as wide, about 0.6 by 1.3 μm . When stained with carbol fuchsin, the spore walls appear reddish purple and quite clear in the center. The spores may form clusters and appear to be stacked. Approximately 2.5 billion spores are produced in each infected larva. If the larva has been infected for less than 10 days, the vegetative cells are present, and some newly formed spores may be seen.

The modified hanging drop technique can be very useful for differentiating American foulbrood from other brood diseases. In areas of the smear where pockets of water are formed in the oil, the spores of *Bacillus larvae* exhibit Brownian movement. This is an extremely valuable diagnostic technique because the spores formed by the other *Bacillus*



Figure 2. Bacterium that causes American foulbrood disease (not to scale): Top, *Bacillus larvae* vegetative cells; middle, *Bacillus larvae* spore formation; bottom, *Bacillus larvae* spores.

species associated with the known bee diseases usually remain fixed (see table 2). It is important to note that Brownian movement can be affected by slide preparation; also, debris and other bacteria can exhibit this motion. Therefore, Brownian movement must not be used as the sole criterion for diagnosis but must be considered together with the characteristic morphology of the spores and the gross larval symptoms. If microscopic examination is not conclusive, cultural tests can be made using the same suspension.

Cultivation of *Bacillus larvae*

Thiamine (vitamin B₁) and some amino acids are required for the growth of *Bacillus larvae*. Routine culture media such as nutrient broth will not support the growth of this organism. Good vegetative growth occurs on Difco brain heart infusion fortified with 0.1 mg thiamine hydrochloride per liter of medium (BHIT) and adjusted to pH 6.6 with HCl, but sporulation does not occur. Satisfactory growth and sporulation occur on the yeast extract, soluble starch, and glucose media recommended by Bailey and Lee (1962). The medium can be liquid, semisolid (0.3% agar), or solid (2% agar). For more information on sporulation, see Dingman and Stahly (1983).

Bacillus larvae spores also reproduce in the hemolymph of honey bee larvae, pupae, and adults when artificially introduced by injection (Michael 1960, Wilson and Rothenbuhler 1968, Wilson 1970).

To culture *Bacillus larvae*, we prepare spore suspensions by mixing diseased material (scales) with 9 mL sterile water in screw-cap tubes. (We use cotton swab applicators to remove and transfer the scales from

Table 2. Differentiation of *Bacillus* species in honey bees

Species	Brownian movement ¹	Catalase production	Nitrate reduction	Growth on nutrient agar
<i>Bacillus larvae</i>	+	—	+	—
<i>Bacillus alvei</i>	—	+	—	+
<i>Bacillus laterosporus</i>	—	+	+	+
<i>Bacillus pulvifaciens</i>	—	—	+	+

¹ In modified hanging drop technique.

the comb to the tubes.) The suspension is heat shocked at 80°C for 10 minutes (effective time) to kill nonsporeforming bacteria. A sterile cotton swab is used to evenly spread a portion of the suspension (approximately 0.2 mL) over the surface of BHIT agar plates, which are then incubated for 72 hours at 34°C. Individual colonies are small (1-2 mm) and opaque; however, if large numbers of viable *B. larva* spores are inoculated, a solid layer of growth will cover the plate.

There are no reliable methods for making plate counts of *Bacillus larva* because fewer than 10 percent of the spores will produce visible growth on the media presently available (Shimanuki 1963). By calibrating our methods using spore and plate counts, we have determined that a minimum of 100 *B. larva* spores are required to produce visible growth on BHIT.


Diagnostic Tests for *Bacillus larva*

Holst Milk Test. The Holst milk test (Holst 1946) is a simple test based on the fact that a high level of proteolytic enzymes is produced by sporulating *Bacillus larva*. The test is conducted by suspending a suspect scale or a smear of a diseased larva in a tube containing 3-4 mL of 1% powdered skim milk in water. The tube is then incubated at 37°C. If *B. larva* is present, the suspension should clear in 10-20 minutes. It should be noted that this test is not always reliable.

Nitrate Reduction. *Bacillus larva* reduces nitrate to nitrite (Lochhead 1937). The nitrate reduction test can be performed on a medium such as BHIT, which contains potassium nitrate (1-2 mg/L of medium). After growth has occurred, the addition of a drop of sulfanilic acid-alpha-naphthol reagent produces a red color if nitrate has been reduced to nitrite. Diagnosis should not be based on this test alone but on this test along with larval gross symptoms, bacterial morphology, and growth characteristics of the bacterial colony.

Catalase Production. A drop of 3% hydrogen peroxide is placed on an actively growing culture on a solid medium. Most aerobic bacteria break down the peroxide to water and oxygen and produce a bubbly foam, but *Bacillus larva* is almost always negative for this reaction (Haynes 1972).

Fluorescent Antibody. The fluorescent antibody technique requires the preparation of specific antibodies stained with a fluorescent dye. Rabbits are injected with pure cultures of *Bacillus larva*, and the active antiserum is collected and stained with a fluorescent dye. This fluorescent antiserum



is mixed with a bacterial smear on a slide and allowed to react. The excess antiserum is washed off the slide, and the slide is then examined with a fluorescence microscope. *B. larvae* appears as brightly fluorescing bodies on a dark background (Toschkov et al. 1970, Zhavnenko 1971, Otte 1973, Peng and Peng 1979).

Viability Test for *Bacillus larvae*

One method of controlling AFB is to destroy the viability of *Bacillus larvae* spores in contaminated bee equipment. This can be accomplished by gamma or electron beam irradiation or by fumigation with a sterilant gas such as ethylene oxide. Assessment of the efficacy of these methods should be based on the number of spores remaining viable in a test sample of brood comb containing at least 10 AFB scales.

A spore suspension is prepared from the sample comb by mixing 10 scales in 10 mL sterile water. Since each scale contains about 2.5 billion spores (Sturtevant 1932), 1 mL of the suspension should contain 2.5 billion spores. A portion of the suspension (0.2 mL = 500 million spores) is spread onto solid BHIT plates as previously described and incubated for 72-96 hours.

The results of the viability tests are reported as the approximate number of viable spores on a per-scale basis. If no colonies form on the medium, the results are recorded as <100 viable spores per scale; 1-9 colonies are recorded as <1,000 per scale; 10-99, <10,000 per scale; over 100 colonies per plate, >10,000 viable spores per scale; and when the plate is completely overgrown with colonies, the results are reported as no detectable reduction of viable spores.

Terramycin (Oxytetracycline) Resistance Tests

Isolates of *Bacillus larvae* can be screened for sensitivity to oxytetracycline based on the size of inhibition zones on agar plates. A spore suspension of the *B. larvae* isolate to be tested is spread on solid BHIT as described previously. A disk (BBL Sensi-Disk) containing 5 µg oxytetracycline is then placed on the plate, and the plate is incubated at 34°C for 72 hours. The zones formed by sensitive strains usually average 50 mm in diameter. Alternatively, oxytetracycline incorporated into liquid BHIT will inhibit the growth of sensitive strains of *B. larvae* at concentrations as low as 12 µg/L of medium (Gochbauer 1953). Care is necessary in making these tests, and adequate control strains should be included.


Any substantial reduction of the zone size or an increase in the concentration of oxytetracycline required to prevent growth of *Bacillus larvae* in liquid medium would be evidence of the development of resistant strains (Gochnauer et al. 1975). However, when interpreting the results of the tests, the effects of growth rates should be considered. Because strains often grow at different rates, one may falsely conclude that a strain is resistant. No resistance of *B. larvae* to oxytetracycline has yet been reported.

Detection of *Bacillus larvae* Spores in Hive Products

Honey. Occasionally it may be necessary to examine honey for the presence of *Bacillus larvae*. Due to the high concentration of carbohydrate and other natural bacteriostatic substance(s) in honey, the examination of honey requires special considerations. The classical method (Sturtevant 1932, 1936) is to dilute the honey 1:9 with water, centrifuge the mixture to concentrate the spores in the sediment, and then examine the sediment microscopically for the presence of spores.

We (Shimanuki and Knox 1988) have developed the following technique to detect *Bacillus larvae* spores in honey. Honey to be examined is heated to 45°C to permit easier handling and to decrease viscosity for more uniform distribution of any spores that may be present. Twenty-five milliliters of honey is placed in a 50-mL beaker and diluted with 10 mL of sterile water. The diluted honey is then transferred into a 1.75-inch (44-mm) dialysis tube. The open end is tied after the tube is filled, and the tube is submerged in running water for 18 hours or in a water bath with three to four water changes in that period. Following dialysis, the contents of the tube are centrifuged at about 2,000 g for 20 minutes. The supernatant is carefully removed with a pipet to leave approximately 1 mL of residue. This residue is resuspended in 9 mL of water in a screw-cap vial and heat shocked at 80°C for 10 minutes to kill nonsporeforming bacteria. Next, 0.5 mL of the suspension is spread onto a plate of BHIT agar. The plate is incubated at 37°C for 72 hours and examined for colonies of *B. larvae*. Difficulties can sometimes occur when honey samples contain other sporeforming bacteria that may completely cover the surface of the plate.

Since approximately 100 *Bacillus larvae* spores are required to produce visible growth on BHIT, this technique can demonstrate the presence of *B. larvae* spores in samples that contain a minimum of 80 spores per mL of undiluted honey (25 mL honey \times 80 spores/mL = 2,000 spores/dialysis = 2,000 spores in 10 mL or 200 spores/mL; 0.5 mL = a 100-spore inocu-



lum). Lower spore levels can possibly be detected by the use of larger honey samples or a second centrifugation to further concentrate the spores.

Pollen. *Bacillus larvae* spores can also be recovered from bee-collected pollen pellets by physically removing bits of AFB scale. A series of sieves of different sizes is helpful. If scales are not detected, one may pass a water-pollen suspension through No. 2 filter paper, centrifuge the filtrate, and culture the pellet as described above (Gochnauer and Corner 1974).

Beeswax. We have had some success in recovering spores morphologically similar to those of *Bacillus larvae* by melting beeswax in boiling water, removing the beeswax cake after cooling, and centrifuging the water at 2,000 g for 20 minutes. The sediment is then examined microscopically for the presence of spores. Spores have also been recovered from contaminated beeswax by chloroform extraction (Kostecki 1969). However, in both cases, positive identification of the spores is not possible because the recovery techniques render the spores nonviable.

European Foulbrood

Melissococcus pluton (= *Streptococcus pluton*) is the bacterium that causes European foulbrood disease (EFB). *Melissococcus pluton* has been reclassified into the new genus *Melissococcus* (Bailey and Collins 1982a and b). However, *Melissococcus pluton* has still not been adequately described to be accepted for the current editions of "Bergey's Manual of Determinative Bacteriology."

Melissococcus pluton is generally observed early in the infection cycle before the appearance of the varied microflora associated with this disease. The *M. pluton* cell is short, nonsporeforming, and lancet shaped. The cell measures 0.5-0.7 by 1.0 μm and occurs singly, in pairs, or in chains (fig. 3).

Cultivation of *Melissococcus pluton*

Melissococcus pluton can be isolated on a medium developed by Bailey (1959). The medium consists of 1 g yeast extract (Difco), 1 g glucose, 1.35 g potassium dihydrogen phosphate (KH_2PO_4), 1 g soluble starch, 2 g agar, and distilled water to make 100 mL; the pH is adjusted to 6.6 with potassium hydroxide (KOH) and the mixture is autoclaved at 10 lb per square inch (116°C) for 20 minutes. It has been found that the addition of cysteine (0.1 g per 100 mL) improves the multiplication of *M. pluton* (Bailey and Collins 1982b).

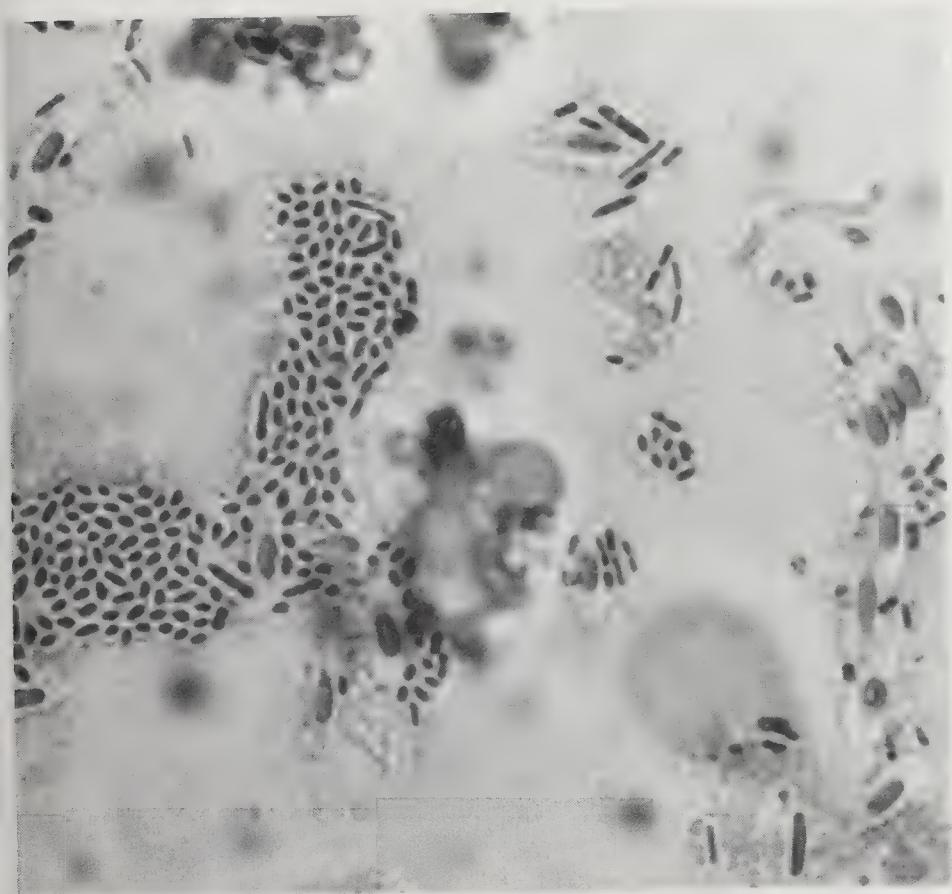


Figure 3. *Melissococcus pluton* and *Bacillus alvei* (X 1200).

It is difficult to isolate *Melissococcus pluton* on artificial media because of its growth requirements and the competition from other bacteria. Also, once isolated, identification of *M. pluton* is difficult due to its pleomorphic nature in culture (fig. 4). *Melissococcus pluton* is best isolated when few if any other organisms are present. According to Bailey (1959), it is best to dry smears of diseased larval midguts on a slide. A water suspension of this material or a suspension prepared from larvae (apparently healthy, infected, or dead), cappings, etc., can be streaked on freshly prepared Bailey's agar medium. Or decimal dilutions of these suspensions can be inoculated into molten Bailey's agar medium (45°C) and poured into plates (Bailey 1981). The plates are incubated anaerobically at 34°C. The "Gas Pak" (BBL) Anaerobic System, including a disposable hydrogen and carbon dioxide generator, is used to obtain anaerobic conditions. Small white colonies of *M. pluton* should appear after 4 days.

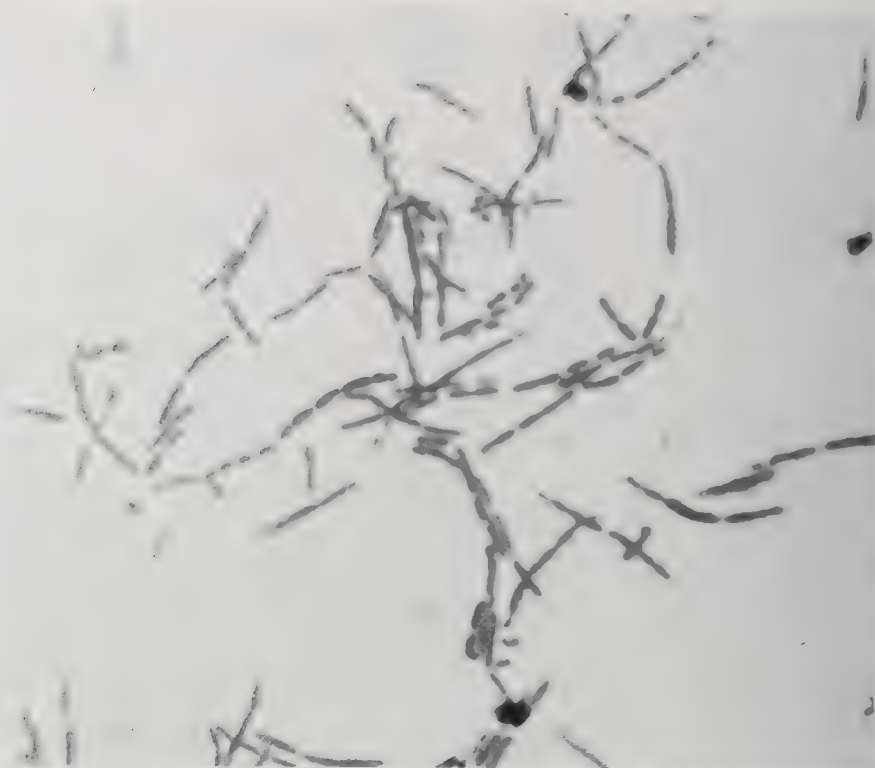


Figure 4. *Melissococcus pluton* as it appears in culture (X 1200).

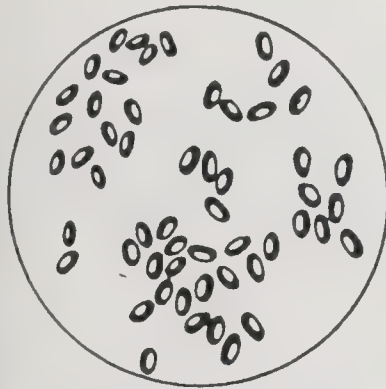
Serodiagnosis

Pinnock and Featherstone (1984) developed an enzyme-linked immunosorbent assay (ELISA) for detecting *Melissococcus pluton*. Using this technique, they were able to demonstrate the presence of *M. pluton* even in apparently healthy honey bee colonies.

Organisms Associated With European Foulbrood

Some organisms do not cause European foulbrood, but they influence the odor and consistency of the dead brood and can be helpful in diagnosis. These secondary invaders include the following:

***Bacillus alvei*.** The bacterium *Bacillus alvei* is frequently present in cases of European foulbrood disease (EFB). It is a rod 0.5-0.8 μm wide by 2.0-5.0 μm long (fig. 5). Spores measure 0.8 by 1.8-2.2 μm . Like *Bacillus larvae*, the spores may be clumped and appear stacked. The sporangium may be observed attached to the spore. Typical strains of *B. alvei* spread



vigorously on nutrient agar and may show "motile colonies"; free spores may lie side by side in long rows on the agar. The growth of this bacterium produces an unpleasant odor.

***Bacillus laterosporus* (= *Bacillus orpheus*).** Rods of *Bacillus laterosporus* measure 0.5-0.8 μm by 2.0-5.0 μm , and the spores 1.0-1.3 by 1.2-1.5 μm (fig. 5). An important diagnostic feature is the production of a canoe-shaped parasporal body that stains very heavily along one side and the two ends, and remains firmly adherent to the spore after lysis of the sporangium. The clear portion with the finely outlined wall is the spore. *B. laterosporus* grows moderately on nutrient agar, becoming dull and opaque, and spreads actively if the agar surface is moist. Growth on nutrient agar with 1% glucose added (glucose agar) is thicker and may become wrinkled.

***Enterococcus faecalis* (= *Streptococcus faecalis* = *Streptococcus apis* = *Streptococcus liquefaciens*).** Ovoid cells (elongated in the direction of chain) are 0.5-1.0 μm in diameter and are usually in pairs or short chains (fig. 5). This organism resembles *Melissococcus pluton* and may exhibit Brownian movement when the modified hanging drop technique is used. Growth occurs on nutrient agar usually within 1 day. Colonies are generally smaller than 2 mm; they are smooth and

Figure 5. Bacteria associated with European foulbrood disease (not to scale): Top, *Bacillus alvei*; middle, *Bacillus laterosporus*; bottom, *Enterococcus faecalis*.

convex, with a well-defined border. When magnified, the colonies appear light brown and granular.

***Bacterium eurydice* (= *Achromobacter eurydice*).** There is no standard description of *Bacterium eurydice*. White (1912) described this organism as a small, slender Gram-negative rod with slightly rounded ends, occurring singly or in pairs and measuring 0.5-1.4 μm long by 0.4-0.7 μm wide. According to White (1920), *Bacterium eurydice* is best isolated by plating the midgut contents of infected larvae on glucose agar and incubating at room temperature. Growth is slow and never luxuriant, and colonies are convex, smooth, and glistening. However, later researchers, who were unable to isolate *B. eurydice* as described by White, used the name *Bacterium eurydice* for a Gram-positive bacterium isolated from diseased larvae. Therefore, mention of the name in the literature causes confusion. This organism is not included in the current editions of Bergey's manual.

***Bacillus apiarius*.** The bacterium *Bacillus apiarius* is rarely encountered and may or may not be legitimately associated with EFB. Rods are 0.6-0.8 μm in diameter and often less at the poles. Special diagnostic features include the ridged, thick, rectangular spore coat and the stainable remnants of the sporangium, which remain attached for a considerable time. Growth can occur on Sabouraud dextrose medium.

Powdery Scale

Bacillus pulvifaciens is the bacterium that causes powdery scale disease. Powdery scale disease is seldom reported, perhaps because the average beekeeper is unable to identify it. A useful diagnostic characteristic is the scale that results from the dead larva. The scale is light brown to yellow and extends from the base to the top of the cell. The scale is powdery; when handled, it crumbles into a dust.

Bacillus pulvifaciens vegetative cells measure 0.3-0.6 μm by 1.5-3.0 μm . The spores are 1.0 by 1.3-1.5 μm . The bacterium can be isolated on nutrient agar, but growth is heavier on glucose agar. When first isolated, the organism produces a reddish-brown pigment that can be lost by subculturing. *Bacillus pulvifaciens* closely resembles *Bacillus larvae*, but the spores do not exhibit Brownian movement in the modified hanging drop technique. Also, *B. pulvifaciens* is distinguished by its ability to grow at 20°C and by its growth on nutrient agar.

Fungal Diseases

Chalkbrood

Ascosphaera apis is the fungus that causes chalkbrood disease.

Ascosphaera apis is a heterothallic organism and develops a characteristic spore cyst when opposite thallic strains (+ and -) fuse. Spore cysts measure 47-140 μm in diameter (fig. 6). Spore balls enclosed within the cyst are 9-19 μm in diameter, and individual spores are 3.0-4.0 μm by 1.4-2.0 μm .

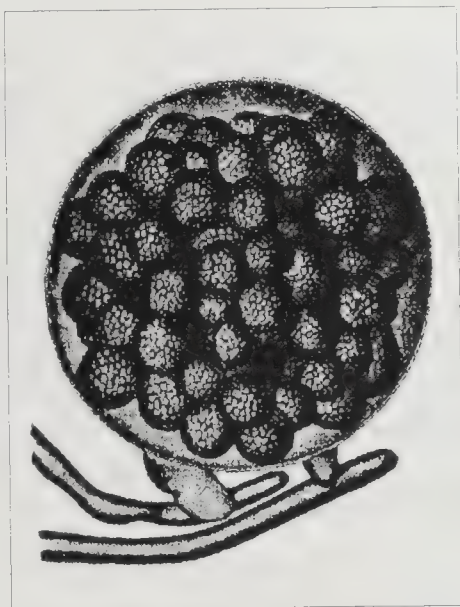


Figure 6. Spore cyst of *Ascosphaera apis* containing spore balls, which in turn contain spores.

Chalkbrood disease can be easily identified by its gross symptoms.

An affected larva becomes overgrown by fluffy cottonlike mycelia and swells to the size of the cell. If only one strain (+ or -) of mycelium is present, the larva dries into a hard, shrunk, white chalklike mummy—thus the name chalkbrood. When the + and - mycelia are present in a diseased larva, spore cysts can form, and the resulting mummies appear either mottled (black on white) or completely black. In heavily infected hives, mummies can be found at the hive entrances or on the bottom boards. Mummies can sometimes be detected in brood cells by tapping the comb against a solid surface. This easy removal of larval remains also differentiates chalkbrood from other brood diseases.

Ascosphaera apis grows luxuriantly on potato dextrose agar fortified with 4 g yeast extract/L. Growth and sporulation also occur on malt agar but less profusely and with no aerial hyphae; this facilitates subculturing and microscopic examination. Cultures have a characteristic fruity odor similar to that of fermenting peaches. The optimum temperature for growth is 30°C.

Ascosphaera apis can be easily isolated from newly infected larvae or fresh mummies. These can be placed directly on the medium and incubated. New mycelial growth is usually visible within 24 hours. Small blocks of agar containing mycelia can be transferred to new plates to obtain pure cultures and isolates of the + and - strains. *A. apis* can be

isolated from old mummies by placing them on water agar (agar with no added nutrients), incubating them, and transferring the new mycelial growth to a nutrient medium. Difficulties sometimes occur because *A. apis* may fail to grow or may be overgrown by other fungi, which can contaminate old mummies.

If only one strain (+ or -) is isolated, a fluffy cottonlike growth will eventually cover the plate. When both the + and - thalli are isolated, spore cysts form throughout the culture. The + and - thalli are morphologically identical. They can be distinguished by inoculating isolates on opposing sides of a plate. When opposite thalli grow together, a line of spore cysts forms at the juncture.

Stonebrood

Stonebrood is usually caused by *Aspergillus flavus*, occasionally *A. fumigatus*, and sometimes other *Aspergillus* species. These fungi are common soil inhabitants that are pathogenic to adult bees, other insects, mammals, and birds. The disease is difficult to identify in its early stages of infection. The fungus grows rapidly and forms a characteristic whitish-yellow collarlike ring near the head end of the infected larva. A wet mount prepared from the larva shows mycelia penetrating throughout the insect. After death, the infected larva becomes hardened and quite difficult to crush—hence the name stonebrood. Eventually, the fungus erupts from the integument of the insect and forms a false skin. At this stage, the larva may be covered with green powdery fungal spores. The spores of *Aspergillus flavus* are yellow green, and *A. fumigatus* spores are gray green. These spores can become so numerous that they fill the comb cells that contain the affected larvae.



Figure 7. Conidial heads of *Aspergillus flavus*.

Stonebrood can usually be diagnosed from gross symptoms, but positive identification of the fungus requires its cultivation in the laboratory and subsequent examination of its conidial heads (fig. 7). *Aspergillus* spp. can be grown on potato dextrose or Sabouraud dextrose agars.



Viral Disease: Sacbrood

Morator aetatulas is the virus that causes sacbrood disease. It is the only common brood disease that is caused by a virus. Since sacbrood-diseased larvae are relatively free from bacteria, laboratory verification is usually based on gross symptoms and the absence of bacteria. Positive diagnosis requires the use of a special antiserum. Affected larvae change from pearly white to gray and finally black. Death occurs when the larvae are upright, just before pupation. Consequently, affected larvae are usually found in capped cells. Head development of diseased larvae is typically retarded. The head region is usually darker than the rest of the body and may lean toward the center of the cell. When affected larvae are carefully removed from their cells, they appear to be a sac filled with water. Typically the scales are brittle but easy to remove. Sacbrood-diseased larvae have no characteristic odor.

Mixed Infections

Bacillus larvae produces a potent antibiotic that eliminates competition from other bacteria typically associated with honey bee larvae. For this reason, American foulbrood and European foulbrood are rarely found in the same colony, except in cases where AFB is just becoming established in colonies that already have EFB.

It is not unusual to find chalkbrood and sacbrood on the same comb or on a comb with larvae infected with AFB. However, no single larva has been found to be infected with more than one disease. This is an important point to remember when selecting a sample for disease diagnosis.

Diseases of Adult Bees

Most diseases of adult bees are difficult to diagnose because the gross symptoms are not unique. For instance, inability to fly, unhooked wings, and dysentery are general symptoms associated with many disorders. In most cases, microscopic examination is required for proper diagnosis.

Protozoan Diseases

Nosema

Nosema apis is the protozoan that causes nosema disease. *Nosema apis* spores are large, oval bodies, 4-6 μm long by 2-4 μm wide (fig. 8). The spores develop exclusively within the epithelial cells of the ventriculus of

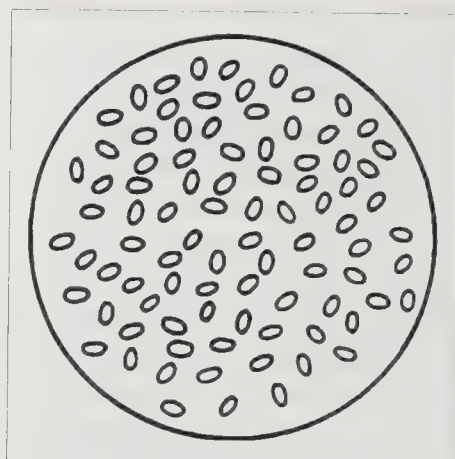


Figure 8. *Nosema* spores as they appear in a wet mount (X 400).

the adult honey bee. *Nosema* disease usually manifests itself in bees that are confined; therefore, the heaviest infections are found in winter bees, package bees, bees used for pollination in greenhouses, etc.

No single symptom typifies *Nosema* disease. Differences between healthy bees and heavily infected bees can be seen by removing the digestive tract and examining the ventriculus. The ventriculus of a healthy bee is straw brown, and the individual

circular constrictions are clearly seen (fig. 9). In a heavily infected bee, the ventriculus is white, soft, and swollen, obscuring the constrictions (White 1918). However, positive diagnosis can be made only by microscopic examination of suspect bees or their fecal material for the presence of *Nosema apis* spores. Samples of bees to be examined can be dried or preserved in alcohol. If the sample is partially decomposed, the presence of yeasts and molds resembling *N. apis* may make an accurate diagnosis difficult. For quick, routine examinations, the abdomens from 10 or more bees are removed, placed in a dish with 1.0 mL water per bee abdomen, and ground with a pestle or the rounded end of a clean test tube. A cleaner preparation can be obtained by grinding free digestive tracts. A wet



Figure 9. Top, Digestive tract from a healthy honey bee. Note the individual circular constrictions on the ventriculus. Bottom, Digestive tract of a honey bee with *Nosema* disease.

mount is prepared from the resulting suspension and examined under the high dry objective of a compound microscope. Alternatively, individual bees can be examined to obtain an approximate percentage of infected bees in a colony. Also, a quantitative measure of levels of *Nosema* infection can be determined using a hemocytometer as described by Cantwell (1970).

Nosema can also be detected without sacrificing workers or queens, by examining their fecal material. A colony can be sampled by collecting feces of worker bees on glass plates near the hive entrance, scraping off a deposit, mixing it with water, and preparing a wet mount from the resulting suspension (Wilson and Ellis 1966). Suspect queens can be held in small petri dishes or in glass tubes and allowed to walk freely. They usually defecate within 1 hour. Queen feces appear as drops of clear, colorless liquid, which are then transferred to a microscope slide with a pipet or capillary tube. A cover glass is placed over the feces before examination with a high dry objective (L'Arrivee and Hrytsak 1964).

Amoeba

Malpighamoeba mellificae is the organism that causes amoeba disease. Since this protozoan is found in the Malpighian tubules of adult bees, diagnosis can be made only by the removal and microscopic examination of the tubules for the presence of amoeba cysts. The cysts measure 5-8 μm in diameter and can be seen in the infected Malpighian tubules (fig. 10).

The Malpighian tubules are long, threadlike projections originating at the junction of the midgut and the hindgut. The tubules can be teased away from the digestive tract with a pair of fine tweezers and then

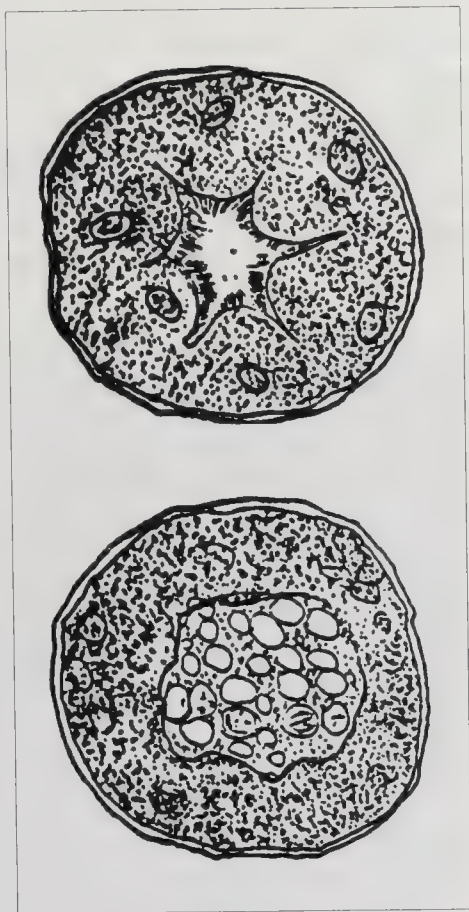


Figure 10. Cross sections of Malpighian tubules. Top, Healthy tubule; bottom, tubule containing cysts of *Malpighamoeba mellificae*.

placed in a drop of water on a microscope slide. A cover glass is positioned over the tubules while applying uniform pressure to obtain a flat surface for microscopic examination. *Malpighamoeba mellificae* can be discerned using a high dry objective and then changing to the oil immersion objective for more detail.

Gregarines

Four gregarines (protozoans of the order Gregarinida) are associated with honey bees: *Monoica apis*, *Apigregarina stammeri*, *Acuta rousseaui*, and *Leidyana apis*. The immature stages, or cephalonts, average about 16 by 44 μm . Cephalonts are oval and consist of two distinct body segments; the posterior segment is larger. The mature stages, or sporonts, average about 35 by 85 μm and have a reduced anterior segment (fig. 11).

Gregarines are found attached to the epithelium of the midgut of adult honey bees. Gently remove the midgut from the digestive tract of a suspect bee and place it on a microscope slide in a drop of water. The midgut can be separated from the digestive tract at the point of attachment with the proventriculus (honey stomach) and hindgut using fine tweezers and a scalpel. Gently break open the midgut with fine tweezers and a probe, and place a cover glass over the resulting suspension. Gregarines can be seen using the low-power objective of a compound microscope.



Figure 11. A gregarine sporont (mature stage).

Flagellates

Crithidia (= *Leptomonas*) species are the flagellates associated with honey bees. Flagellates have been found either free in the lumen or attached to the epithelium of the hindgut and rectum of adult honey bees (Fyg 1954). Flagellates vary in size from 5 to 30 μm . Some appear as pearlike bodies with flagella; others are long threadlike forms or are round without flagella (Lotmar 1946). To look for flagellates, remove the digestive tract of a suspect bee and place it on a microscope slide in a drop of water. Then, using fine tweezers and a scalpel, separate the hindgut and rectum at the point of attachment with the midgut. Macerate the hindgut and rectum, using a fine pair of tweezers and a probe. Place a cover glass on the resulting suspension and observe under the high dry objective of the microscope.

Bacterial Diseases

Septicemia

Pseudomonas aeruginosa (= *Pseudomonas apiseptica*) is the bacterium that causes septicemia in honey bees. This disease results in the destruction of connective tissues of the thorax, legs, wings, and antennae. Consequently, the affected bees fall apart when handled. Dead or dying bees may also have a putrid odor.

Pseudomonas aeruginosa rods measure 0.5-0.8 by 1.5-3.0 μm . They are Gram-negative and occur singly, in pairs, or in short chains. A bacterial smear and Gram stain can be easily prepared after removing a wing from the thorax and dipping the wing base in a drop of water on a microscope slide. To isolate this organism, streak the base of a wing across Difco *Pseudomonas* isolation agar or *Pseudomonas* Agar F. The optimum temperature for growth is 37°C. *Pseudomonas aeruginosa* in culture is characterized by the excretion of diffusible yellow-green pigments that fluoresce in ultraviolet light (wavelength below 260 nm).

Septicemia disease can also be diagnosed by reproducing the disease symptoms in healthy caged bees. This is accomplished by preparing a water extract (macerate the equivalent of one suspect bee per mL of water) and inoculating healthy bees through the thorax (see Methods) or dipping them in the water extract. Bees with septicemia die within 24 hours and exhibit the typical odor and the “break apart” symptom after approximately 48 hours.

Spiroplasmosis

Spiroplasma species is the bacterium that causes spiroplasmosis.

Spiroplasma is a helical, motile, cell-wall-free prokaryote that is found in the hemolymph of infected adult honey bees. The organism is a tiny, coiled, and sometimes branched filament 0.7-1.2 μm in diameter (fig. 12). Its length increases with age and ranges from 2 to >10 μm (Clark 1977, 1978a).

Spiroplasma can be seen in the hemolymph using the oil immersion objective of a phase-contrast microscope. Hemolymph can be taken from adult bees by puncturing the intersegmental membrane directly behind the first coxae with a fine capillary tube made from the tip of a Pasteur pipet.

This organism can be cultured in standard mycoplasma broth medium (GIBCO) and in Singh's mosquito tissue culture medium with 20% fetal calf serum.

Viral Diseases

Chronic Bee Paralysis

Bees affected by chronic bee paralysis are usually found on the top bars of the combs. They appear to tremble uncontrollably and are unable to fly.



Figure 12. *Spiroplasma* species (X 21,840).



In severe cases, large numbers of bees can be found crawling out the hive entrance. Individual bees are frequently black, hairless, and shiny. However, in some cases, paralysislike symptoms can be caused by toxic chemicals.

Ideally, the diagnosis of paralysis disease is made using serological techniques. Since this is beyond the capability of most laboratories, diagnosis is usually made by observing symptoms in individual bees and, when possible, colony behavior.

Paralysis disease can be diagnosed by reproducing the disease symptoms in caged bees. This can be done by spraying, feeding, or injecting a water extract made from the suspect bees. The extract is prepared by macerating the equivalent of one suspect bee in 1 mL of water. It is then centrifuged to eliminate large suspended matter and passed through a 0.45- μ m filter to remove bacteria. To feed up to 20 caged bees, mix 2 mL of the extract with an equal volume of sugar syrup. For inoculation, each bee receives 1 μ L of the extract through a dorsal abdominal intersegmental membrane (see Methods). The symptoms of paralysis should be visible after 6 days. Appropriate control bees should be treated with extracts made from healthy bees.

Filamentous Virus

Filamentous virus is also known as F-virus and bee rickettsiosis. This disease, previously thought to be of rickettsial origin, can be diagnosed by examining the hemolymph of infected bees using phase-contrast microscopy. The hemolymph of honey bees infected with this virus is milky white and contains many spherical to rod-shaped viral particles of a size close to the limit of resolution for light microscopy. The viral particles consist of a folded nucleocapsid within a viral envelope (fig. 13) and are 0.4 by 0.1 μ m (Clark 1978b).

Noninfectious Disorders

Noninfectious disorders can be the result of neglect, lethal genes, pollen or nectar from poisonous plants, toxic chemicals (pesticides), etc. Most often, dead or discolored pupae result from a noninfectious condition. For a good review of noninfectious diseases, see Tucker (1978).

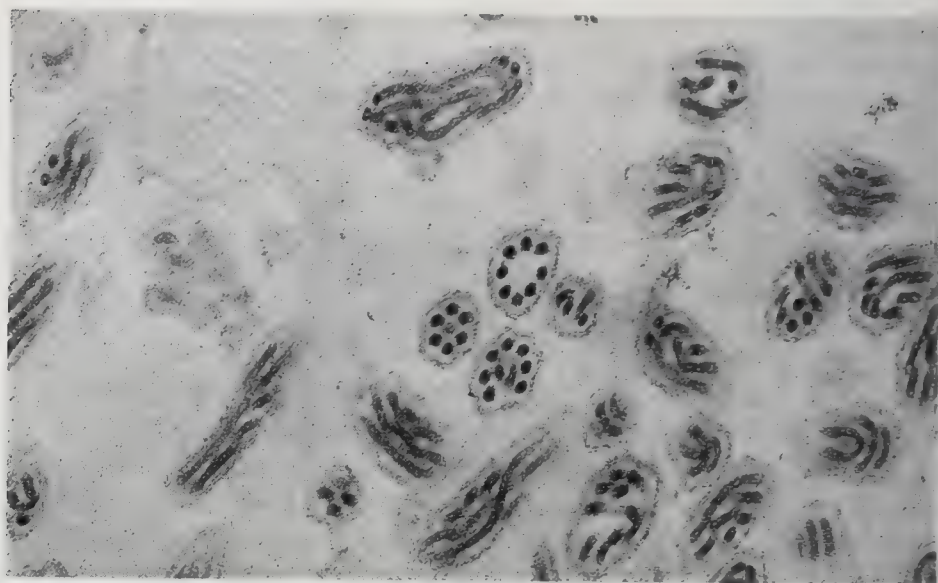


Figure 13. Filamentous virus (X 67,250). Each viral particle consists of a nucleocapsid enclosed in a viral envelope.

Neglected Brood

Normally nurse bees feed and protect the brood. However, if there is a sudden shortage of adult bees, the larvae and pupae suffer and may die of chilling, overheating, or starvation.

Chilled Brood

Chilling usually occurs in early spring when brood nests expand rapidly and there is a shortage of adult bees to cover all the brood. Consequently, chilled brood is found most often on the fringes of the brood area and healthy brood at the center. However, chilling can also happen during cold weather following any sudden reduction of the worker bee population. Chilled larvae and pupae are often yellowish, tinged with black on segmental margins. They may also be brownish or black, crumbly, pasty, or watery. In extreme cases, brood cells are punctured and uncapped, and pupae are decapitated by the adult bees. It should be remembered that decapitation can also result from the larvae of the lesser wax moth.

Overheated Brood

The overheating of brood develops when there is a sudden loss of worker bees available to cool the colony during hot weather. Larvae that died



from overheating become brownish or black and are watery; pupae have a black, greasy appearance. Newly emerged adult bees may be wingless. Cappings of brood cells can appear melted, darkened, sunken, and punctured.

Starved Brood

Normally when there is shortage of food in a colony, larvae are removed and/or consumed by the adult bees. However, when there is a sudden shortage of adult bees available to feed the larvae, the larvae starve. Affected larvae are not restricted to the periphery of brood combs. The most striking feature of starved brood is the larvae crawling from the brood cells in search of food. Starved brood is almost always restricted to the larval stage. However, emerging bees may starve if they were stressed as pupae by chilling or overheating and if there are too few nurse bees to feed them soon after they have chewed through their cappings. These bees usually die with only their heads out of the cells and with their tongues extended.

Overheated Bees

Overheating in worker bees can occur when bees are confined in their hives during hot weather without proper ventilation or access to water. Bees dying from overheating crawl about rapidly while fanning their wings. They are often wet, and their wings appear hazy. In some cases, an abnormally large accumulation of dead bees may be seen at the hive entrance.

Genetic Lethality

Bees can also die from genetic faults during all stages of development, usually without exhibiting symptoms of known diseases. However, drone brood from laying workers and drone-laying queens often die with symptoms resembling EFB but in the absence of known pathogenic agents. Genetic lethality is the suspected cause of this condition.

Plant Poisoning

Poisonous plants can be a problem under certain conditions in limited areas. If a plant's nectar is poisonous, the symptoms of plant poisoning are limited to the blooming period of the plant. However, if the poison is in the pollen, the symptoms may linger as long as the pollen remains in the combs. There is no clear-cut method for differentiating between plant poisoning and pesticide poisoning. The effects of plant poisoning are

usually more gradual and last longer than the effects of pesticide poisoning. Plant poisoning usually occurs in the same geographical area at the same time each year, whereas pesticide poisoning is indiscriminate. For a good review of poisonous plants, see Barker (1978). Some examples of plant poisoning are listed below and in table 3.

Purple Brood

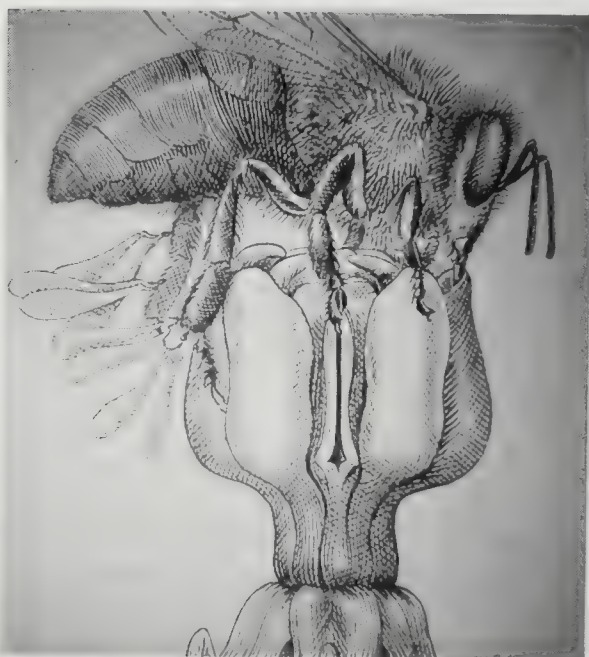
Purple brood occurs when adult bees collect and use the pollen and nectar from *Cyrilla racemiflora* (titi, southern leatherwood). This "disease" is characterized by the blue or purple color of the affected larvae.

Paralysis

Aesculus californica (California buckeye) is probably the best known of the poisonous plants in the United States. Field bees exhibit symptoms similar to those of chronic bee paralysis; i.e., the bees are black and shiny from loss of hair and they tremble. Also, either the eggs do not hatch or the larvae die soon after hatching.

Milkweed Pollinia

The pollen of milkweed (*Asclepias* species) is produced in pollinia (coherent pollen grains) that are attached in pairs by a slender filament.



When removed from a flower, the pollinia resemble a wishbone with pollen masses hanging from the ends. Honey bees become ensnared in the thin pollinia attachment and free themselves by pulling the pollinia from the flower (fig. 14). Honey bees often become seriously encumbered and unable to effectively fly or crawl because of the structures that remain attached to their body parts.

Figure 14. Milkweed pollinia attached to honey bee.

Source of poison	Stages most affected	Effect on adult	Effect on brood	Effect on colony
Toxic chemicals	Adult	Field bees die in or near hive or in field. Nurse bees may also die. Queens usually not affected.	Usually few larvae killed. Symptoms of starvation may be evident if adult population reduced severely.	Weakened or killed. Many dead bees near hive.
California buckeye (<i>Aesculus californica</i>)	Young brood	Emerging young workers often deformed, pale. Some hairless and tremble. Queens lay eggs at reduced rate, cease, or become drone layers.	Eggs normal at outset; later fail to hatch or all are drone eggs. Larvae die soon after hatching and disappear. Little or no capped brood; if present, scattered.	Weakened or killed. May be many dead bees near entrance. Supersedure of queen may fail.
Yellow jessamine (<i>Gelsemium sempervirens</i>)	Larva, pupa, and young adult	Young workers affected and soon die. Old adults appear normal.	Pupae die in cells and become mummified.	Slightly to severely weakened.
Loco plants (<i>Astragalus</i> spp.)	Adult and pupa	Field bees die. Some become black and tremble. Queen may die.	Many cells contain dried pupae.	Population dwindles. Colony may die.
False hellebore (<i>Veratrum californicum</i>)	Adult	Many field bees die between plants and hive. Adults die in curled state. Queens not affected.	No effect.	Field population lost.
Southern leatherwood (<i>Cyrilla racemiflora</i>)	Larva	No effect.	Many blue or purple larvae. Larvae die in cells when nearly mature.	Slight to severe weakening.

Source: Modified from Burnside and Vansell (1936).



Pesticide Poisoning

The most apparent indication of serious pesticide poisoning is the sudden loss of adult bees. This loss is characterized by the appearance of many dead and dying adult bees and sometimes pupae at the colony entrances. However, in many instances, the bees are lost in the field before returning to the colony. If the pesticide is brought back to the hive by the foragers, the nurse bees are killed when they feed on contaminated honey or pollen and the brood will exhibit symptoms of neglect or poisoning. The symptoms of poisoned honey bees often depend on the class of pesticide involved (table 4).

A residue of a pesticide may be present as the original pesticide, or as an identifiable degradation product, or both. Frequently, the amount of residue is extremely small. Pesticide analysis consists primarily of the following (from Wilson et al. 1980):

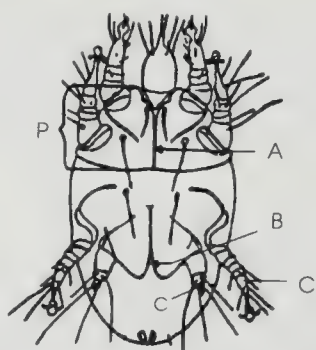
- (1) Blending and extraction of the biological material (such as bees or pollen) with a suitable solvent system to maximize the recovery of suspected pesticides and their metabolites. This eliminates the bulk of the biological substrate.
- (2) A series of liquid-liquid extractions and column chromatographs to further separate the residues from other materials of biological origin. A very fast method for cleanup is gel permeation chromatography. Large molecules of biological origin emerge from the column first, thereby directly trimming the crude extract down to a much cleaner sample.
- (3) Detection of residues at the highest possible sensitivity to avoid interference from substances not previously removed. The most popular detection system is gas-liquid chromatography, wherein the residue-containing sample is volatilized and chromatographed as a vapor. Thin-layer and paper chromatography are also useful for establishing the identity of pesticide residues. Visualization for detection usually involves spraying the chromatograms with a chemical that reacts with the pesticide or metabolite to produce a characteristic color. Other methods used for residue analysis include mass spectroscopy and fluorometric techniques. The residue must be capable of absorbing visible light or ultraviolet light. The intensity of the reemitted light is measured at some suitable wavelength and compared with standards.

Class of pesticide	Examples of pesticides	Symptoms of poisoning
Organo-phosphorous	Parathion, methyl parathion, dimethoate (Cygon), naled (Dibrom), mevinphos (Phosdrin), diazinon, dichlorvos (Vapona), monocrotophos (Azodrin), malathion, tepp, phorate (Thimet), phosphamidon (Dimecron), chlorpyrifos (Dursban)	Regurgitation (bees are wet); disorientation, lethargy. Perhaps distended abdomen, erratic attempts to clean selves, tumbling about, paralysis, ultimately death. Wings held away from body but usually remaining hooked together. High percentage of poisoned bees die at colony.
Chlorinated hydrocarbon	Aldrin, chlordane, DDT, dieldrin, heptachlor, lindane, toxaphene	Erratic movements, abnormal activities, trembling. Hindlegs dragging as if paralyzed and wings held away from body but usually remaining hooked together. High percentage of poisoned bees die in field as well as at colony.
Carbamate	Carbaryl (Sevin), carbofuran (Furadan), aminocarb (Matacil), dimetilan (Dimetilane), mexacarbate, methomyl (Lannate, Nudrin)	Aggressiveness, erratic movements; then inability to fly, stupefaction as though chilled; followed by paralysis, morbidity, death. Most bees usually die at colony. Queens often cease egg laying; hive bees initiate super-secture, rearing queens before egg laying resumes.
Dinitrophenyl	Dinocap (Karathane), DNOC, DNOCHP, DNOSBP	Similar to symptoms of chlorinated hydrocarbons but often accompanied by regurgitation of substances in digestive tract, as is typical of organophosphorous pesticides. Most affected bees usually die at colony.
Botanical	Pyrethrum, allethrin, and the pyrethroids: resmethrin, bioresmethrin, bioethanomethrin, and cismethrin; also nicotine, rotenone, ryania, sabadilla	Perhaps regurgitation from highly toxic pyrethroids, together with erratic movements; then inability to fly and stupefaction, followed very soon by paralysis, moribundity, and death. Bees often die between foraging area and colony.

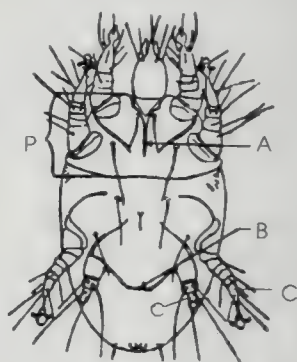
Source: Modified from Atkins (1975).

Parasitic Honey Bee Mites

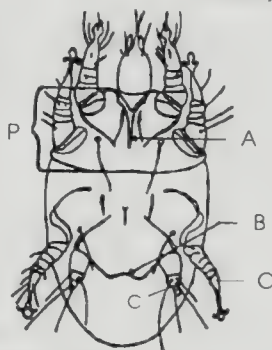
Three *Acarapis* species are associated with adult honey bees: *Acarapis woodi*, *A. externus*, and *A. dorsalis*. These mites are difficult to detect and identify because of their small size and similarity; therefore, they have frequently been identified by location on the bee instead of by morphological characters. Only *A. woodi* can be diagnosed solely on habitat; the position of other species on the host is a useful but not infallible characteristic. *Acarapis woodi* lives exclusively in the prothoracic tracheae; *A. externus* inhabits the membranous area between the posterior region of the head and thorax or the ventral neck region and the posterior tentorial pits. *Acarapis dorsalis* is usually found in the dorsal groove between the mesoscutum and mesocutellum and the wing bases. Morphological characters separating these species are shown in figure 15. Complete descriptions and illustrations are in Delfinado-Baker and Baker (1982).



***Acarapis dorsalis*:** Apodeme (A) full length of propodosoma (P); coxal plate (B) deep indentation; tarsal joints (C) $< 10\ \mu\text{m}$.



***Acarapis externus*:** Apodeme (A) 2/3 length of propodosoma (P); coxal plate (B) variable indentation; tarsal joints (C) $> 10\ \mu\text{m}$.



***Acarapis woodi*:** Apodeme (A) 2/3 propodosoma (P); coxal plate (B) shallow indentation; tarsal joints (C) $< 10\ \mu\text{m}$.

Figure 15. Morphological characters separating *Acarapis* species.

Honey Bee Tracheal Mite (*Acarapis woodi*)

The female *Acarapis woodi*, or honey bee tracheal mite, is 143-174 μm long and the male 125-136 μm . The body is oval; widest between the second and third pair of legs; and whitish or pearly white with shining, smooth cuticle. A few long hairs are present on the body and legs. This mite has an elongate, beaklike gnathosoma with long, bladelike styles (mouthparts) for feeding on the host.

The population of *Acarapis woodi* may vary seasonally. During the period of maximum bee population, the number of bees with mites is reduced. The likelihood of detecting tracheal mites is highest in the fall. In sampling for this mite, one should try to collect either moribund bees that may be crawling near the hive entrance or bees at the entrance as they are leaving or returning to the hive. These bees should be placed in 70% ethyl or methyl alcohol as soon as they are collected. One should not collect bees that have been dead for an unknown period because they are less than ideal for the diagnosis of tracheal mites.

No one symptom characterizes this disease. An affected bee could have disjointed wings and be unable to fly, or have a distended abdomen, or both. Absence of these symptoms does not necessarily indicate freedom from mites. Positive diagnosis can be made only by microscopic examination of the tracheae; since only *Acarapis woodi* is found in the bee tracheae, this is an important diagnostic feature.

A healthy trachea appears cream color or white. The trachea of a severely infested bee has brown or black blotches with crustlike lesions and is obstructed by many mites in different stages of development (fig. 16). The trachea must be examined carefully for the presence of mites. The trachea may not always be discolored when mites are present, and a cloudy or discolored trachea does not always contain mites.

Methods for diagnosing *Acarapis woodi* are listed below. Each of these methods has its advantages and disadvantages.

Method 1

Pin the bee on its back and remove the head and first pair of legs by pushing them off with a scalpel or razor blade in a downward and forward motion (fig. 17). Using a dissecting microscope, remove the first ring of the thorax (tergite of prothorax) with forceps. This exposes the tracheal

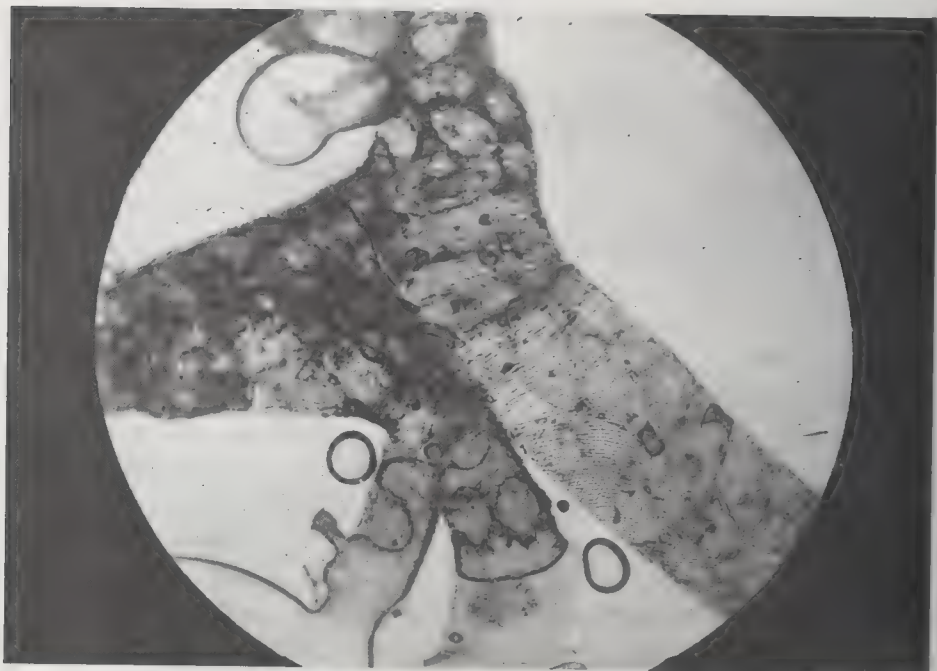


Figure 16. Trachea containing mites (X 40).

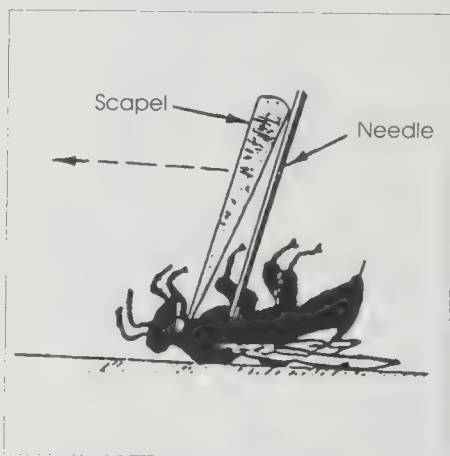


Figure 17. Positioning a bee for dissection.

trunks in the mesothorax (fig. 18). When the infestation is light, it is necessary to remove the trachea. Place the trachea in a drop of lactic acid on a glass slide for clearing, and cover with a cover glass for examination at X 40-100 on a compound microscope.

Method 2

Grasp the bee between your thumb and forefinger and remove the head and first pair of legs. Then with a scalpel, razor blade, or fine pair of

scissors, cut a thin transverse section from the anterior face of the thorax in such a way as to obtain a disk. Place the disk on a microscope slide and add a few drops of lactic acid. This makes the material more transparent and also helps to separate the muscle. With the aid of a dissecting microscope, carefully separate the muscles, remove the trachea, and examine the preparations as in method 1. This procedure is recommended for quick examination of a few bees.

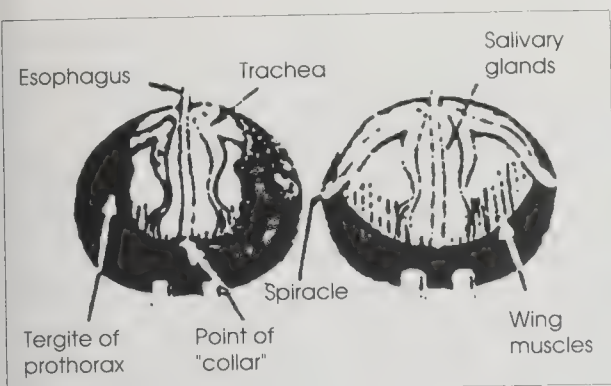


Figure 18. Location of the trachea in the thorax.

Method 3

Cut a few thoracic disks as described in method 2, place them on a slide, and add a few drops of 10% potassium hydroxide (KOH). Heat the slide gently for 1-2 minutes (do not boil), cover with a cover glass, crush the disks lightly, and examine microscopically. This procedure is advantageous when the bees have been dead for some time.

Method 4

Prepare transverse-section disks from the thoraces of 50 honey bees as described in method 2, place them in 5% KOH, and incubate at 37°C for 16-24 hours. The KOH dissolves the muscle and fat tissue, leaving the trachea exposed. Then examine the disk-trachea suspension under a dissecting microscope. Remove suspicious tracheae from the disks and examine the tracheae microscopically (X 40-100). This procedure is recommended for large samples of bees.

Method 5

Remove the heads, abdomens, wings, and legs from 20-200 thoraces and place them in a homogenizing jar with 25 mL of water. Homogenize three times for several seconds at 10,000 rpm, using just enough water to rinse the inside of the jar. Then strain the suspension through a 0.8-mesh sieve and rinse with water. The final volume of the filtrate should be about 50 mL. Centrifuge the filtrate at about 1,500 g for 5 minutes and discard the supernatant. Then add a few drops of lactic acid to the preparation, and allow it to stand for 10 minutes. Finally, place the sediment on a slide for examination. In this method, a microscope with an oil immersion objective is required to correctly identify *Acarapis woodi* because other mites associated with honey bees are morphologically similar. This technique is described by Colin et al. (1979).



Method 6


In the flotation method (Camazine 1985), bees cannot be stored or killed in alcohol. For cleanest preparations, remove the head, wings, legs, and abdomen (saving only the thoraxes) of recently killed bees. This removal is easily done using one's fingers when the bees are frozen. Place 25-100 bees in a household blender with enough water added to cover the blades. Blend the preparation for no more than 15 seconds, just until the thoraxes are broken apart. (Blending for longer periods will pulverize the tracheae.) Pour the resulting mixture into a series of test tubes (2-3 cm in diameter). Most of the denser muscle fibers and cuticular fragments fall to the bottom while the tracheae and air sacs float, forming a thin whitish layer on the surface of the water. Suction off this layer with a pipette, place on one or more slides, and cover with cover slips. Examine the slides under a compound microscope at X 100-250. Examine the slide in a systematic manner for darkened, blotchy, and discolored tracheae and for undamaged tracheae that may also contain mites and eggs.

Method 7

In the modified methylene blue staining technique (Peng and Nasr 1985), prepare transverse-section disks from the thoraxes of 50 bees as described in method 2. Place the disks in a beaker of 8% KOH solution, and heat to boiling with continuous gentle stirring of the disks. Remove the solution from the heat and continue stirring until the soft tissues inside the disks are dissolved and cleared (about 10 minutes). Excessive stirring and heating will damage the specimens and subsequently reduce the color intensity of the mites. Recover the disks from the KOH by filtration through a perforated Tissue-Tek processing capsule. After filtration, cover the processing capsule with a lid, place in a beaker, and wash with tap water to remove the remaining KOH. After washing, transfer the processing capsule to a modified methylene blue staining solution (prepared by first dissolving 1% aqueous methylene blue and then adding sodium chloride to make a 0.85% sodium chloride solution). Immerse the capsule in that solution for 5 minutes and then in distilled water for 2-5 minutes; finally, rinse the capsule with 70% ethyl alcohol. Examine the disks for stained mites within the tracheae under a dissecting microscope at X 10-25.

Method 8

Differentiation of live mites from dead mites (Eischen et al. 1986) is the method of choice for evaluating chemicals used to control tracheal mites.



Anesthetize live bees with carbon dioxide and remove the abdomens with a scalpel to prevent being stung during examination. Remove the head and first pair of legs of each bee by holding the bee on its back and gently pushing this section off with a downward and forward motion. Place each bee, held in this position, under a dissecting microscope, and remove the first ring of the thorax with fine forceps. This exposes the tracheal attachment to the thoracic wall, which is often the only location of mites in a light infestation. Remove tracheae that appear abnormal with tweezers and transfer to a glass slide containing a thin film of glycerol. Then dissect the tracheae using a pair of fine needle probes. Mites are considered dead if they do not move; also, dead mites often appear discolored and desiccated. Living mites have a translucent gray or pearl color and move within a few seconds after dissection.

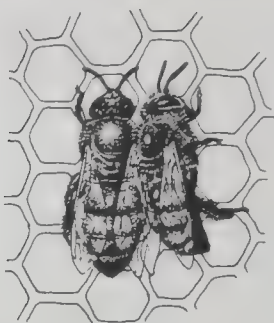
Method 9

For serodiagnosis, Ragsdale and Furgala (1987) produced an antiserum against extracts of *Acarapis woodi*-infested tracheae to be used as the primary antibody in a direct enzyme-linked immunosorbent assay (ELISA). Ragsdale and Kjer (1989) improved the ELISA technique, making it as reliable as dissection for the detection of *A. woodi*. Their ELISA is accurate, sensitive, reproducible, cost effective, rapid, and easy to use.

Varroa jacobsoni

The mite *Varroa jacobsoni* can be found on adult bees, on the brood, and in hive debris. The most severe parasitism occurs on the older larvae and pupae, with drone brood being preferred to worker brood (Ritter and Ruttner 1980). In heavy infestations, pupae may not develop into adult bees. The adults that do emerge may have shortened abdomens, misshapen wings, and deformed legs and may weigh less than healthy bees (De Jong et al. 1982b).

The adult female mite is oval and flat, about 1.1 mm long and 1.5 mm wide, and pale to reddish brown; it can easily be seen with the unaided eye. The mites attach to the adult bee between the abdominal segments or between body regions (head, thorax, abdomen) and are therefore difficult to detect. However, they can be easily recognized against the white surface of pupae. Male mites are considerably smaller and are pale to light tan (Delfinado-Baker 1984). The life cycle of *V. jacobsoni* is summarized in figure 19.



10

Mites transfer through close contact between bees.



1

Adult bee, with *Varroa* feeding on hemolymph



9

Adult females leave cell with emerging bee. Male and immature stages stay in cell.



8

Mating within cell

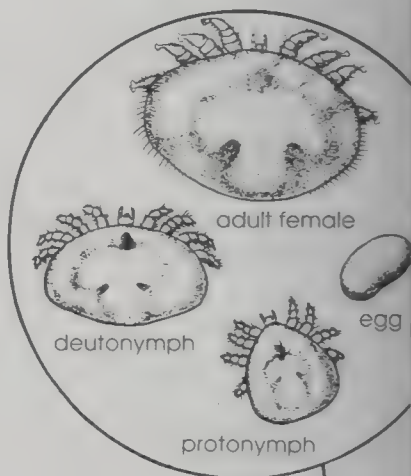


5-6 days
adult male



7

7-8 days
adult female



adult female

deutonymph

egg

protonymph

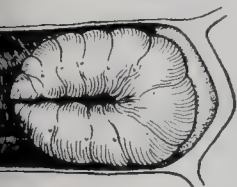


6

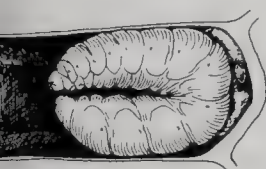
1-6 eggs developing from egg to larva to protonymph to deutonymph

Figure 19. Life cycle of *Varroa jacobsoni*. (Courtesy of Roger A. Morse.)

Illustrated by B. Alexander



enters cell with
of 5 to 5-1/2 days.



3
Mite in bee food



te feeds on prepupa.



male lays first egg
hours after cell
pping. Female lays
sequent eggs at
-hour intervals.

It is important to note that the bee-louse, *Braula coeca*, resembles *Varroa jacobsoni* in size and color. However, *Braula*, being an insect, has six legs that extend to the side (fig. 20). *Varroa*, an arachnid, has eight legs that extend forward (fig. 21).

When sampling, remember that the number and location of mites in a colony vary according to time of year. The number of mites is lowest in spring, increases during summer, and is highest in fall. During spring and summer, most mites are found on the brood (especially drone brood). In late fall and winter, most mites are attached to adult worker bees.

Methods of Examining Adult Honey Bees

For a sample of adult honey bees, 500 to 1000 bees should be collected. This can be done by brushing honey bees off the comb through a large-mouthed funnel (of paper or cardboard, etc.) into a container or by using a modified portable car vacuum cleaner. Individual honey bees can be examined with or without the aid of a hand lens or a dissecting microscope. When the mites are moving about on a bee, they are fairly easy to detect; but once they attach themselves between segments, they are difficult to find. Mites can be detected and collected by three methods, as follows:

Shaking Method

Varroa jacobsoni can be dislodged by shaking the bees in liquids such as hot water, alcohol, detergent solution, hexane,

Figure 20.
Braula coeca,
dorsal view.

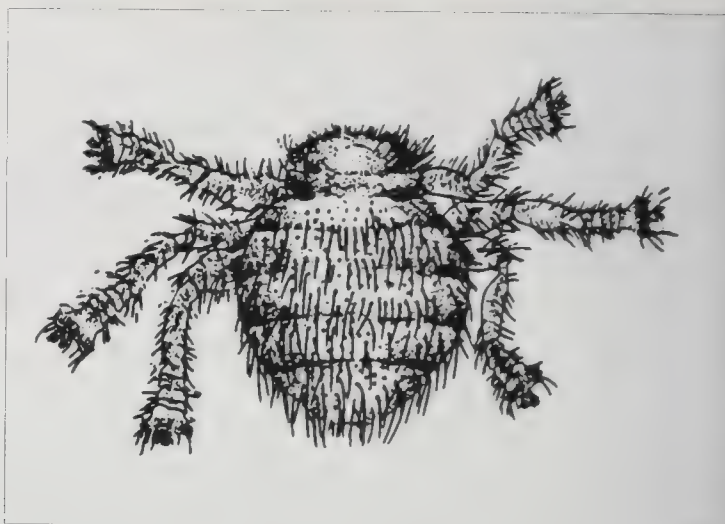


Figure 21.
Varroa jacobsoni,
ventral view.



gasoline, or diesel fuel. We recommend 70% alcohol (ethyl or isopropyl) because some of the other materials are dangerous or difficult to use. The alcohol kills and preserves the bees for other purposes, such as examination for *Acarapis woodi*. De Jong et al. (1982a) found that hand-shaking bees in alcohol for 1 minute dislodged about 90% of the mites and that mechanical shaking on a rotary shaker for 30 minutes removed 100% of the mites. The mites are collected by passing the bees and alcohol through a wire screen (8- to 12-mesh) to remove the bees and then sieving the alcohol through a 50-mesh screen or cotton cloth. The screen or cloth is then examined for mites.



Ether Method

This technique is a rapid and efficient detection method in the field and avoids the handling, shipping, and time-consuming procedures associated with shaking adult bees in alcohol or other solvents. The bees (500-1,000) are collected in a jar and anesthetized with ether delivered from an aerosol can (this aerosol product is sold in auto-parts stores as an aid to start engines). A 1- to 2-second burst of material is adequate. The bees are then rotated in the jar for about 10 seconds. The majority of mites will have dislodged from their hosts and should be adhering to the inside wall of the jar. To complete the process, the bee sample is deposited on a white surface and spread around. This should cause any remaining mites to fall onto the white substrate. The bees should be examined immediately after the application of ether because the mites tend to stick to the bees if left in the jar for more than a few minutes. Alternatively, the bees can be left in the jar to which alcohol is added for laboratory shaking and preservation.

Heating Method

Live adult honey bees can be shaken into a wire-based cage and placed in an oven over white paper. The bees are heated for 10-15 minutes at 46°- 47°C. Then *Varroa jacobsoni*, if present, can be observed on the white paper (Crane 1978).

Methods of Examining Brood

To look for mites on brood, the pupae (preferably drone) are examined. *Varroa jacobsoni* can be easily seen against the white surface of worker or drone pupae after they are removed from their cells. It is suggested that a minimum of 100 drone pupae per colony be examined. The pupae can be collected by one of the following methods:

- The classic method of pupal collection is to uncap each cell and then remove the pupae with forceps or a hive tool.
- Groups of pupae can be quickly and easily removed from their cells by inserting a capping scratcher at an angle through the cappings and lifting the brood and cappings upward (Szabo 1989).
- With a long-bladed knife, the caps are sliced off an area of brood 4-6 square inches. The comb (frame) is then sharply jarred on a hard, flat, white surface such as a hive top. The brood will fall onto the white surface, and the mites can be easily observed.

- The brood comb can be incubated at 37°C, followed by examination of all the emerged bees and remaining brood.

Methods of Inspecting Hive Debris

Debris in a hive (such as wax particles, pollen, dead bees and brood, and mites) normally falls to the hive floor and is removed by house-cleaning bees during warm weather. This material can be collected and examined for the presence of *Varroa jacobsoni* as follows:

- The collection of hive debris can be facilitated by white construction paper on the hive floor. The paper is stapled under a wood (1/4-inch) and wire (8- to 12-mesh) frame, which protects the paper and debris from the bees. The paper is examined for mites, which can be easily seen against the white background. A magnifying glass or dissecting microscope can be helpful in locating the mites in the debris. Sticky boards or shelf paper (with the adhesive surface exposed) instead of construction paper will help hold the debris.
- The acaricides used to treat mite infestations can also be applied to bee colonies in combination with the paper method to detect *Varroa jacobsoni*. Apistan is currently approved and available for this purpose. After treatment, the mites drop to the paper and can be easily detected. It is important that the paper have a sticky surface (see previous paragraph) to hold any recovering mites.
- A flotation method can be used to examine debris for *Varroa jacobsoni*. Hive debris is placed in a jar or pan and covered with 98% alcohol. The mites float to the surface while the heavier debris sinks (Ritter and Ruttner 1980).
- Mites can sometimes be collected in dead bee or pollen traps attached to the colonies.

Tropilaelaps clareae

The distribution of *Tropilaelaps clareae* (fig. 22) is still restricted to Southeast Asia. These mites also parasitize adult bees and brood, and they have been reported to infest colonies infested with *Varroa jacobsoni* (Delfinado-Baker and Aggarwal 1987). Female mites are about 1 mm long and 0.6 mm wide; the male is slightly smaller. These mites are difficult to detect because of their small size and their brownish color, which blends perfectly with brood cappings and comb. *Tropilaelaps*

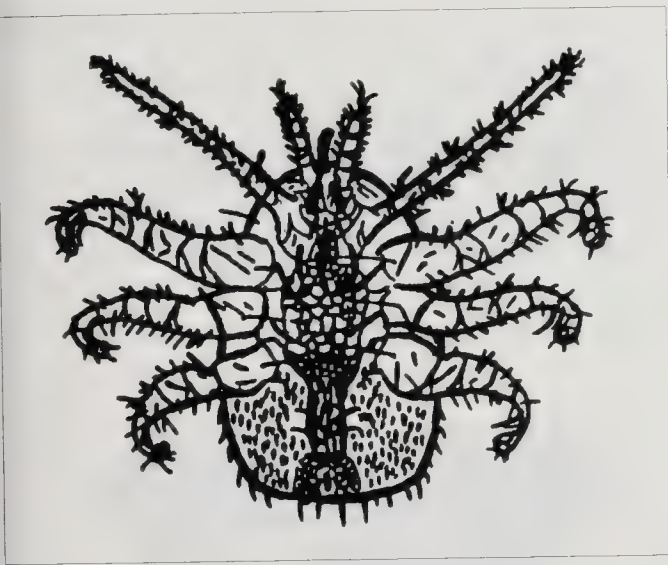


Figure 22.
Tropilaelaps clareae,
ventral view.

clareae can be found by observing under a magnifying glass or a dissecting microscope a brood comb suspected of being infested. In the field, when the comb is hit on a light-colored surface, dislodged mites may be seen moving on that surface. The mites can be picked up with a fine brush moistened with alcohol.

Pests

Wax Moths

The greater wax moth, *Galleria mellonella* (fig. 23), is the most serious pest of honeycombs. Comb damage can also be caused by the lesser wax moth, *Achroia grisella* (fig. 23), and the Mediterranean flour moth, *Anagasta kuehniella*. These moths are an especially serious problem in tropical and subtropical climates, where warm temperatures favor the rapid development of the moths. Female greater wax moths lay their eggs in a cluster, usually in the cracks or between the wooden parts of the hive. The larvae of the moths are the destructive stage. They actually obtain nutrients from honey, castoff pupal skins, pollen, and other impurities found in the beeswax, but not the beeswax itself. Consequently, older combs are more likely to be infested than new combs or foundation.

Bee-louse (*Braula coeca*)

Braula coeca, or bee-louse (fig. 20), is actually not a louse but a wingless fly that feeds on honey. No detrimental effect on adult bees has been attributed to the bee-louse, but its larvae can damage the appearance of

Figure 23. Greater wax moth, *Galleria mellonella* (top), and lesser wax moth, *Achroia grisella* (bottom) (not to scale).

These species are easily distinguished from each other by shape of the wings and comparative sizes. Greater wax moth is about two times larger than lesser.



comb honey. Adult bee-lice can be found on adult workers and queens. It is important to note that *Braula coeca* resembles *Varroa jacobsoni* in size and color. However, *Braula*, being an insect, has six legs that extend to the side. *Varroa*, an arachnid, has eight legs that extend forward.

Melittiphis alvearius

Melittiphis alvearius is a little-known mite that is associated with adult honey bees but is not considered to be a pest. It is unlikely that *M. alvearius* would be confused with other mites found in honey bee colonies. The adult female mite is ovate, flattened dorsoventrally, 0.79 mm long and 0.68 mm wide, brown, and well sclerotized with numerous stout and spinelike setae. It is included here because it was found in California during a survey for *Varroa* and because of increasing reports on its distribution (Delfinado-Baker 1988).

Appendix A. Directions for Sending Diseased Brood and Adult Honey Bees for Diagnosis

The accuracy of the diagnosis of any bee disease depends on the condition of the sample. Mail the sample in a wooden or heavy cardboard box. The sample can be loosely wrapped in a paper bag, paper towel, newspaper, etc. Avoid wrappings such as *plastic bags*, *aluminum foil*, *waxed paper*, *tin*, or *glass* because they allow fungi to grow on the samples. Samples are accepted from anyone and in most cases are processed within one working day.

How to Address and Package Samples

- Send all samples to

Bee Disease Diagnosis
USDA, ARS, Bee Research Laboratory
Building 476, BARC-East
10300 Baltimore Avenue
Beltsville, MD 20705-2350.

- A short description of the problem along with your name and address should accompany the sample. Also, your name and address should be plainly written on the top of the box.

Samples of Brood

- The sample of comb should be about 4 square inches.
- The sample should contain as much of the dead or discolored brood as possible.
- NO HONEY SHOULD BE PRESENT IN THE SAMPLE.
- If a comb cannot be sent, the probe used to conduct a ropiness test may contain enough material for tests. The probe can be wrapped in paper and sent to the laboratory in an envelope. However, this method is unsatisfactory for verification of sacbrood disease, which requires special antisera. We rely on gross symptoms for this diagnosis.



Samples of Adult Honey Bees

- Send at least *100 bees* in a sample.
- If possible, select bees that do not appear normal or that died recently. Decayed bees are not satisfactory for examination.
- Bees submitted for the identification of mites should be placed in 70% ethyl or methyl alcohol as soon as possible after collection. These samples should be in leak-proof containers.

Appendix B. Identification of Africanized Honey Bee

BRL Protocol for Identification of Africanized Honey Bee


FABIS, as described in the “Fast Africanized Bee Identification System (FABIS) Manual” (Sylvester and Rinderer 1987), will be used as a screening method to identify European bees. The full 26-character morphometric analysis will be conducted on all samples of honey bees not identified as European by FABIS. Therefore, when the Bee Research Laboratory (BRL) declares a sample Africanized, the identification is the result of the full 26-character morphometric analysis and is definitive.

Submission of Honey Bees to BRL for Identification of Subspecies

It is assumed that most honey bee samples submitted for identification of subspecies will be from Animal and Plant Health Inspection Service, Plant Protection and Quarantine (APHIS-PPQ). Samples will also be accepted from State regulatory personnel by prior arrangement. A sample of 100 bees should be submitted. Anyone submitting suspected Africanized honey bees should understand our priorities for identification and sample submission. They are as follows:

Priority No. 1: Swarms (colonies) anywhere in the United States involved in severe stinging incidents.

Priority No. 2: Any swarms (colonies) in the United States that have been pretested and identified as non-European by FABIS.



Honey bees submitted for identification should be placed in 70% ethyl or methyl alcohol as soon as possible after collection. Each sample should consist of at least 100 workers in leak-proof containers and be sent directly to

Bee Disease Diagnosis
USDA, ARS, Bee Research Laboratory
Building 476, BARC-East
10300 Baltimore Avenue
Beltsville, MD 20705-2350.

A short history of the problem along with the sender's name, address, and telephone number should accompany the sample. If results are urgently required, please advise the Laboratory by telephone (301-344-2205) of the shipment and send the sample via *Express Mail*.

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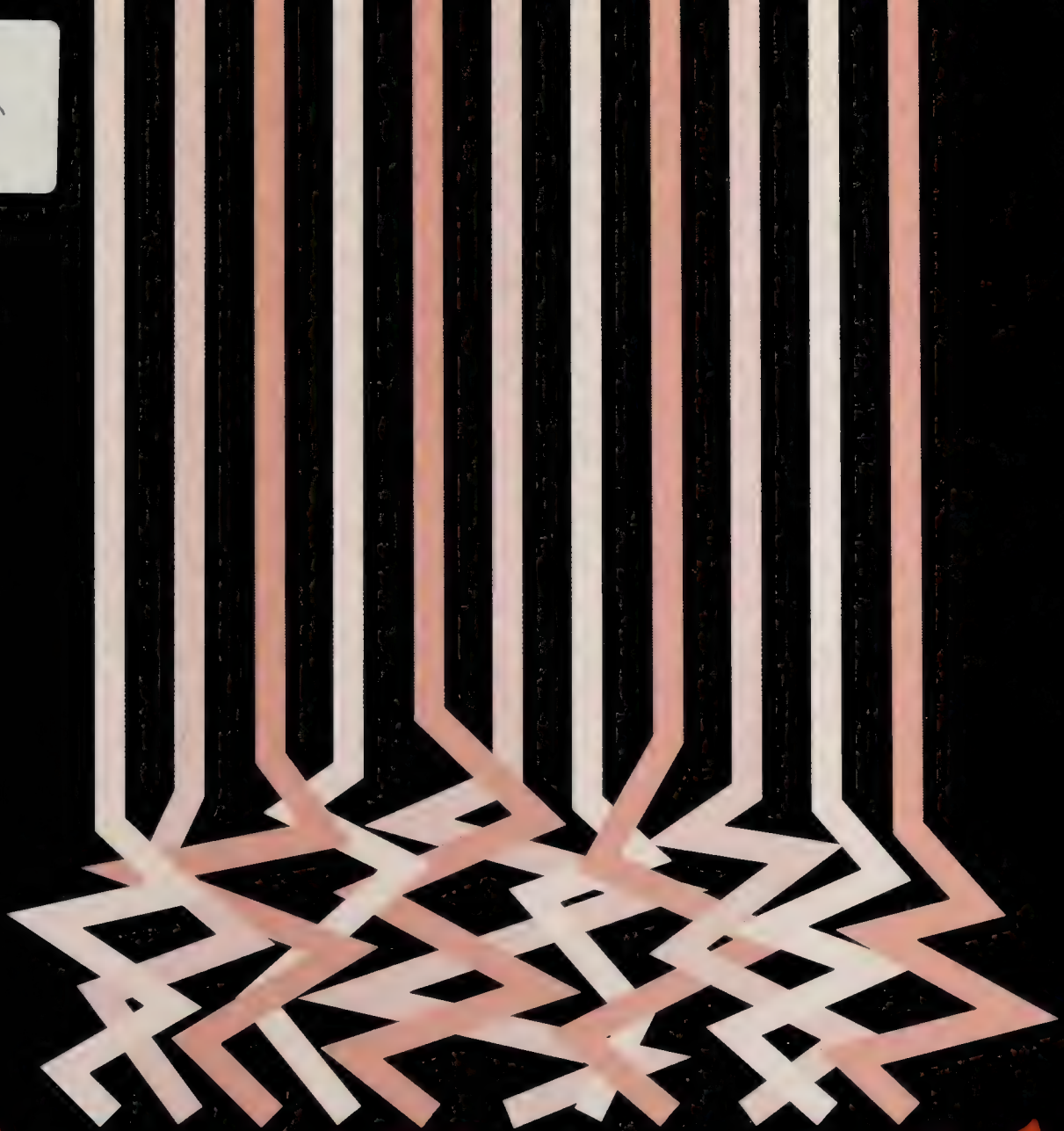
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ARMILLARIA ROOT DISEASE

by

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Preface

Armillaria root disease has been the object of intensive basic and applied study by pathologists, physiologists, taxonomists, and others since Robert Hartig published his classical work in 1874. Even with this immense collective effort, persistent confusion has obscured the real significance of *Armillaria* as a pathogen. Only recently have pathologists accepted that *Armillaria* comprises numerous species with distinct distributions and pathogenicities. This treatment resolves many contradictory claims and observations made about *Armillaria* species and the often serious root diseases they cause.

Armillaria is, however, more than just a serious pathogen. Economic importance aside, *Armillaria* possesses many fascinating biological attributes that are broached in this volume. These include bioluminescence; antibiotic and alcohol production; multiple morphological forms including rhizomorphs; in vitro fructification; peculiar mycorrhizal associations with the roots and tubers of some achlorophyllous plants; an unusual nuclear cycle; and others. In our view, the amplitude of this variability makes species of *Armillaria* well suited as experimental organisms for studying fungal development, physiology, genetics, and speciation.

Through this volume we strive to synthesize the available information on the taxonomy, physiology, and life history of *Armillaria* spp. This material is further developed to clarify the impacts, dynamics, management, and control of the root diseases caused by various species of *Armillaria* in diverse natural and exotic forests, orchards, and amenity plantings throughout the world.

The book begins with a discussion of the taxonomy and nomenclature of *Armillaria* species. Through this treatment, we not only learn how to correctly refer to these organisms but also discover why so much confusion has surrounded their taxonomy and nomenclature. This leads into chapter 2 wherein the concept and sig-

nificance of biological species are explored as are the sexual patterns and life cycle of the fungus. The nutritional, biochemical, and physiological requirements of the fungus and the biochemical basis for its interactions with hosts are considered in chapter 3. Attributes of inoculum and the infection process are discussed in chapter 4. Disease symptoms and diagnosis, both on individual trees and in stands, are treated in chapter 5. Pathogenicity and various ways of assessing it are discussed in chapter 6. The next three chapters consider the role of stress factors in promoting disease and address disease development in natural forests and manmade plantations. Chapter 10 introduces mathematical modeling as a means to quantify disease development and to predict the consequences of various management actions. Chapter 11 presents management and control methods, including recent information on antagonistic organisms.

This book was conceived through discussions on *Armillaria* held among members of the International Union of Forestry Research Organizations' Working Party on Root and Butt Rots of Forest Trees. This is one of the largest, oldest, and most active IUFRO groups. Many members of that group have authored chapters for this book; many others provided ideas, advice, and encouragement. The volume stands as a tribute to the spirit of international cooperation in forestry research that is fostered by IUFRO.

The worldwide interest in, and importance of, *Armillaria* root disease is reflected by the contributions to this volume: 24 authors from 9 nations. Managing not only the vast amount of manuscript provided by these authors but also their often contrasting ideas, opinions, and personal reflections into a single volume with some meaningful composition and structure became our unique challenge.

Our ambition has been and remains the presentation of accurate information about *Armillaria*. Clarity of expression became the driving objective we used as a final arbiter for many difficult decisions. We wanted to remove as many potential disruptions to smooth reading as possible yet preserve an international character. Thus, we retained words and expressions unique to certain countries or cultures, but we imposed uniform spelling and punctuation standards throughout all chapters. We also sidestepped standard botanical nomenclature.

For general discussion in the text, we chose where possible to use common names as established in standard references. Coping with genus, specific epithet, authorities and multiple revisions, plus abbreviations, parentheses, and brackets proved extraordinarily tedious during manuscript preparation and revision. Ultimately, we judged the nomenclature system to be too clumsy to meet our objective of clear expression. We met the obligation for scientific accuracy by adding an Appendix which cites in alphabetical order both Latin and common names with the appropriate standard references. To overcome nomenclatural problems with reference to various *Armillaria* species, we used specific epithets only where investigators have identified their isolates. We used the generic term "*Armillaria*" where identity is uncertain.

The timing of this work seems particularly important as our knowledge of these organisms and the diseases they cause has increased markedly in recent years. We hoped that by compiling the information at this time we could stimulate and help focus further research while also providing a basis for wise and informed management of *Armillaria* diseases.

In addition to an analysis, synthesis, and consolidation of the vast literature that has accumulated, as well as the advancement of concepts and insights to assist future research on *Armillaria*, this volume celebrates the many achievements of the past. We believe this Handbook on *Armillaria* root disease will be of interest and value to graduate students, mycologists, pathologists, and forest managers for many years.

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Dedication

Robert Hartig (1839-1901)

The 'Father of Forest Pathology,' who concluded that wood decay was caused by microorganisms and provided convincing evidence for the pathogenicity of several fungi attacking trees. His monographic treatment of *Agaricus melleus* in *Wichtige Krankheiten der Waldbäume* (1874) has had an enduring influence on the perceptions of pathogenic behavior and study of *Armillaria*. A detailed account of Hartig's remarkable contributions to forest pathology is found in the American Phytopathological Society, English translation of this work (Phytopathological Classics No. 12, 1975).



A



B



C



D

Characteristics of *Armillaria* root disease. A: Infection of a seedling by rhizomorphs from an inoculum segment colonized by *Armillaria*; B: Mycelial fan in the cambial region at the base of a recently killed tree. Such fans can be diagnostic of tree death by *Armillaria*; C: *Armillaria* infection center in pole-sized ponderosa pine showing disease progression through the stand; D: Signature on an aerial photograph of an *Armillaria* root disease infection center. (C.G. Shaw III, R. Williams)

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Nomenclature, Taxonomy, and Identification

Roy Watling, Glen A. Kile, and Harold H. Burdsall, Jr.

Confusion has surrounded the nomenclature and taxonomy of the genus *Armillaria* (Fr.:Fr.) Staude for over a century. Until recently, taxonomists have consistently disagreed on the exact description of the genus and its correct name according to the International Code of Botanical Nomenclature. This confusion has created uncertainty for taxonomists and plant pathologists, and has hindered the study of this widely distributed and economically important genus of fungi. Based on the analyses of Watling and others (1982), we consider the genus to be a natural grouping, and that *Armillaria* is the appropriate generic name. This conclusion has been widely accepted since that publication (Antonin 1986, Bérubé and Dessureault 1988, Guillaumin and others 1985, Intini 1988, Marziano and others 1987, Rishbeth 1983, Roll-Hansen 1985, Romagnesi and Marxmuller 1983, Termorshuizen and Arnolds 1987).

The first record of an *Armillaria* species was probably either in 1729 (Micheli) or 1755 (Battarra). However, not until the later classical authors began to describe the larger fungi could several taxa now assigned to *Armillaria* in its restricted sense (*Armillaria sensu stricto*) be unequivocally recognized. From the pathologists' viewpoint, confusion has arisen from the assumption of many authors that *Armillaria mellea* (Vahl: Fr.) Kummer is a single variable or polymorphic species (Singer 1956) that occurs in both temperate and tropical regions. Although this contention is supported by maps purporting to show worldwide distribution (Distribution of Plant Diseases 143, 3rd ed. 1969) and by host lists on an international or local basis (Laemmlen and Bega 1974, Pegler and Gibson 1972, Raabe 1962a), classical European authors such as Bolton (1788-91) realized that several taxa were involved.

European interest in morphological studies of *Armillaria* was renewed in the 1970's (Romagnesi 1970, 1973, 1978; Singer 1970a,b; Singer and Clemencon 1972). The demonstration of a bifactorial sexual incompatibility system in an *Armillaria* species (Hintikka 1973) led to studies that showed several intersterile

groups, termed "biological species", could be recognized in Europe (Korhonen 1978, 1980) although, as such, "biological species" had no standing within the International Code of Botanical Nomenclature. Anderson and Ullrich (1979) expanded this approach using North American isolates. Morphological and genetic data have subsequently been combined to link many biological species to morphological species and vice versa (see chapter 2). Many laboratories now consistently test interfertility to identify unknown vegetative isolates.

Armillaria probably contains about 40 species, of which several may have restricted geographical distributions or vegetation associations. The movement of phanerogams or their products from one area of the world to another may, however, have extended distributions of some species.

Species of *Armillaria* are necrotrophic pathogens of plants, and in one case of another agaric, and mycotrophic associates of achlorophyllous plants (see chapter 8). Some ecological niches recorded for members of the genus are undoubtedly exploited by several species, but the formerly broad concept of *A. mellea* applied by many authors has confounded recognition of the species involved. Retaining voucher specimens of basidiomes¹ and vegetative isolates from phytopathological studies is thus extremely important. Although the ability to identify species of *Armillaria* has advanced rapidly only in recent years, we have accumulated a wealth of observational and experimental information on various aspects of *Armillaria* biology which makes it one of our better-known genera of Agaricales.

Nomenclatural and taxonomic aspects of *Armillaria* in general and the European species in particular have been amply described in recent years (Antonin 1986,

¹The term basidiome is used in this publication in preference to less specific terms such as basidiocarp, carpophore, fructification, fruit body, fruiting body, sporocarp, sporophore (Maas Geesteranus 1971).

Guillaumin and others 1985, Herink 1973, Marxmüller 1987, Roll-Hansen 1985, Romagnesi and Marxmüller 1983, Termorshuizen and Arnolds 1987, Watling 1987, Watling and others 1982). This chapter provides an introductory survey of the major issues in the nomenclature and taxonomy of the genus.

***Armillaria* (Fr.:Fr.) Staude— Nomenclature and Typification**

In Fries' *Systema Mycologicum* (1821), 12 species, including *Agaricus melleus*, were accepted in the tribe *Armillaria*, which he had established 2 years earlier (Fries 1819). The tribes *Armillaria* and *Lepiota* were later combined (Fries 1825) with the latter name used for the enlarged group. However, Fries (1838) reverted to *Armillaria* for some species. By this time, the number of species in the tribe had doubled, but its scope remained unchanged in his later *Monographia Armillariarum Suecicae* (Fries 1854).

Staude (1857) was the first to raise Fries' tribe to generic rank. Singer (1951b, 1955a,b, 1986) has disputed whether Staude's entry meets all the requirements for valid publication, but Staude is now generally accepted as the validating author of the genus (Donk 1949, 1962; Watling and others 1982). Singer (1951b, 1955a,b) proposed Kummer (1871) as the correct author for *Armillaria*, and has recently reiterated that belief (Singer 1986), a conclusion we do not accept. Thus, Singer (1986) has argued that the publication of Staude (1857) is inadmissible according to the International Code of Botanical Nomenclature, but nothing has changed since Donk (1949, 1962) clearly discussed the status of Staude's account. Watling and others (1982) found no reason to disagree with Donk's findings. Both Staude and Kummer (1871) include within their generic concept *Agaricus melleus*, and as far as anyone can decide from the available information, it agrees with that outlined within Fries' (1821) tribe *Armillaria*. Fries (1821; p. 26) includes a reference to Battara (1755) under synonymy of tribe *Armillaria* but nowhere discusses this entry further. We think that this one mention can hardly support Singer's statement "defines the basic scope of the tribus." Nothing in Fries (1821) or in Battara (1755) necessitates further exploration, and this re-emphasizes the importance of *Systema Mycologicum* (Fries 1821) in forming a clear base line. Clements and Shear (1931) subsequently selected it as type species for the genus in their comprehensive survey of the nomenclature of the genera of fungi.

Following Staude's authority for *Armillaria*, the genus follows in a straightforward manner. Staude (1857) included four species: *Ag. melleus*, *Ag. melleus*, *Ag. aurantius*, and *Ag. robustus*.

The last two are now considered species of *Tricholoma* (Fr.) Staude, and *Ag. mucidus* is placed in *Oudemansiella* Spegazzini (or *Mucidula* Pat.). Adopting either *Ag. aurantius* or *Ag. robustus* as the type could lead to *Armillaria* becoming a synonym of *Tricholoma*. Kuhnner (1988) suggested *Ag. mucidus* as the type, but this was never recommended by any earlier author. This choice would be unfortunate as *Ag. mucidus* has little in common with *Ag. melleus*. The selection of *Ag. melleus* as type by Clements and Shear (1931), Dennis and others (1954), and Donk (1949, 1962) was supported by Watling and others (1982). *Agaricus melleus* Vahl:Fr. is based on *Icones plantarum, Flora Danica* (1792), vol. 6(17): 9, plate 1013 (1790), M. Vahl (fig. 1.1) [= *Armillaria mellea* (Vahl:Fr.) Kummer in *Der Fuhrer in die Pilzkunde* (1871)]. As no herbarium specimen was available to support this plate, neotypic material was designated (Watling and others 1982).

The generic name *Armillariella* (Karsten 1881) typified by *Ag. melleus* has been used in many publications; if *Armillaria* is based on a species other than *Ag. melleus*, *Armillariella* would become available. Karsten's genus is logical if *Armillaria* is typified by *Ag. luteovirens* Alb.



FIGURE 1.1 — *Agaricus melleus*, as illustrated by Martin Vahl in *Flora Danica* (1790 - 1792). Marxmüller and Printz (1982) considered this figure could also represent *Armillaria borealis*, although Marxmüller (1987) accepted it as *Agaricus melleus*.

& Schw.:Fr., as supported by Singer (1951a). However, this species was not originally in Fries' tribe, a prerequisite for consideration. *Armillariella* is therefore an obligate synonym of *Armillaria*. *Floccularia* Pouzar is the correct genus for *Ag. luteovirens* and its allies.

Incorporating *Armillaria* into *Clitocybe* (Fr.) Staude has sometimes blurred the identity of what we believe to be a natural genus. While first proposed by Ricken (1915), French mycologists have most frequently followed this approach, for example Kühner and Romagnesi (1953) and Heim (1950, 1963). The latter included tropical species of *Armillaria* in his concept of *Clitocybe*. This proposal does not interfere with typification, as *Armillaria* would simply become a synonym of *Clitocybe*. However, clear differences exist in basidiome development between *Armillaria* and *Clitocybe* (Watling and others 1982). Additionally, Bennell and others (1985) showed radical differences in basidiospore wall morphology between *A. mellea* and *Clitocybe nebularis* (Batsch:Fr.) Kummer. *Clitocybe tabescens* (Scop.:Fr.) Bres. is the species usually cited as a link between the two genera. It is similar to *A. mellea* in basidiome development, basidiospore wall structure, and its bifactorial heterothallism (Anderson 1982). This species is thus best placed in *Armillaria*, probably as *A. socialis* (DC:Fr.) Herink [synonym *A. tabescens* (Scop.:Fr.) Emel.].

Singer (1951a) and Herink (1973) suggested subcategories of the genus. Singer divided *Armillaria* (as *Armillariella*) into two sections distinguished by the presence or absence of a veil (annulate and exannulate species), a subdivision he later maintained (Singer 1986). Herink (1973) followed Singer and recognized *Armillaria* as an annulate subgenus and *Desarmillaria* as an exannulate subgenus. He placed *Armillaria mellea* in the first and *A. socialis* in the second. His ideas agree with our own concepts, although we believe it will eventually be possible to subdivide the subgenus *Armillaria* into related subgroups.

Generic Characteristics

Various morphological, cultural, and other features help distinguish *Armillaria* from other genera of Agaricales. Collectively, these characters define the genus, and variations among them define species. The following are the salient characteristics of *Armillaria*:

Habit — clitocyboid with slightly sinuate, adnexed, subdecurrent or decurrent gills; bivelangiocarpic or metavelangiocarpic development in annulate species, apparently monovelangiocarpic development in exannulate species; solitary, gregarious, or caespitose.

Pileus — fleshy, thinning towards margin,

expallant, hygrophanous or not; color variable yellow-brown, yellow-olivaceous, ochraceous, rusty-tawny, umber, cigar brown, less commonly buff or clay pink, sometimes ivory, pallid, or even mouse-gray; surface glabrous, scurfy, squamulose, squamules darker than ground color, sometimes restricted to disc; glabrescent as scales are lost; dry or becoming viscid to distinctly viscid, in some species almost glutinous.

Stipe — central, fibrous-fleshy, not characteristically cartilaginous; often becoming hollow and the outermost layers splitting and curling back to expose flesh; more or less annulate with floccose-membranous to arachnoid veil; often arising from sheets of white mycelia or from well-differentiated black rhizomorphs, and/or, associated with plaques of thin, black, tough tissue.

Lamellae — close to subdistant; moderately thick; nearly white, ivory, or cream-color at first but frequently becoming spotted with cinnamon-buff, rusty-tawny, or sometimes, particularly with age, with a tinge of purple or distinctly pink; sinuate; adnexed to deeply decurrent.

Flesh — of pileus pale and of stipe white at first, becoming as dark as umber or Vandyke brown downwards and sometimes tinted red or bluish at base where colonized by pigment-producing bacteria or nectriaceous fungi.

Spore-print — white to cream-color darkening slightly on drying, and in herbarium material.

Basidia — 4-spored, sometimes 2-spored; thin-walled; with or without a basal clamp-connection; hyaline; smooth-walled in aqueous alkali solutions or if thick-walled [= crassobasidia (Chandra and Watling 1983)] then appearing silvery or glassy, and/or, becoming ochraceous or fulvous.

Basidiospores — ellipsoid; inamyloid; hyaline, yellowish cream-color or ochraceous in aqueous alkali solutions; weakly cyanophilic; thin to moderately thick-walled; smooth or slightly verruculose or rugulose with broad, blunt usually prominent apiculus; lacking germ-pore or apical differentiation (thinning or thickening).

Cheilocystidia — present or absent, often inconspicuous; variable in shape sometimes catenulate-septate; thin-walled or becoming slightly thick-walled with age sometimes with apical prolongation and with or without basal clamp-connection; smooth; hyaline to honey-colored in aqueous alkali solutions.

Pleurocystidia — absent or, if present, thin-walled; poorly differentiated and rarely visible above the level of the basidia.

Pileipellis — an irregular, disrupted trichodermium consisting of (i) an irregular, easily destroyed *suprapellis* composed of groups of fulvous or cinnamon, subparallel, ascendant, loosely to strongly

adhering hyphae intermixed with broad, frequently encrusted hyphae (which form the scales), often with clamp-connections; ascendant hyphae becoming repent to form a rather amorphous adnate layer; (ii) *mediopellis* - of parallel to subparallel hyphae forming a cutis that may or may not gelatinize but sooner or later becomes the outermost layer; and (iii) *subpellis* - a compact hyphal layer.

Stipitipellis — parallel hyphae overlain by more or less strongly developed, irregular, filamentous velar remnants; in parts of stipe free from velar material showing development of cylindric to elongate clavate or lageniform caulocystidia.

Pileus and stipe trama — monomitic; hyphae inamyloid, generally lacking clamp connections.

Hymenophoral trama — bilateral at first and remaining so or becoming regular with age although always demonstrating some divergent arrangement; constitutive hyphae generally lacking clamp-connections; inamyloid.

Vegetative growth — variable on agar media but typically reddish-brown crustose surface mycelium; usually slow growing; with or without tufts of cinnamon aerial mycelium; with or without reddish-brown rhizomorphs or with white to cream-color rhizomorphs embedded in the medium with emergent reddish-brown tips; rhizomorphs branch monopodially, dichotomously, or irregularly; vegetative mycelium often bioluminescent; cells uni- or multinucleate; nuclei apparently diploid.

Rhizomorphs — mycelial aggregations with a melanized outer layer and pale, apical growing tip; produced in culture and from infected lignicolous material.

Single basidiospore isolates — from heterothallic species typically slow growing; producing white, fluffy to cottony mycelium, sometimes with areas of brown or reddish; with or without sparse rhizomorph development; nuclei haploid.

Compatibility system — bifactorial; heterothallic with multiple alleles at the incompatibility loci; some species possibly homothallic.

Relationships With Other Agarics

Modern classifications of the Agaricales link *Armillaria* s.s. with the Tricholomataceae (Jülich 1981; Kühner 1980; Singer 1951a, 1986). However, even in the temperate northern hemisphere where the agarics have been most intensively studied, only Jülich (1981) indicated a strong relationship between *Armillaria* and another genus in the Tricholomataceae, *Tricholomopsis* Singer. Possible relationships to the Cystodermataceae (Romagnesi 1980), the Entolomataceae (Bennell and Jülich 1985), and the Amanitaceae (Helfer and Watling 1989) also have been discussed.

The many distinctive morphological characteristics of the genus, the production of characteristic rhizomorphs, both parasitic and saprophytic capabilities, and the apparently diploid nuclei in the vegetative mycelium (see chapter 2), lead us to believe that it stands quite distantly from other agaricoid genera. Thus, Jülich's (1981) introduction of the family Armillariaceae to accommodate the genus has great merit.

Relationships Within *Armillaria*

Apart from the subgeneric distinction between developmental patterns in annulate and exannulate species and its inference of relatedness, no systematic attempt has been made to assess the phylogeny of species based on differences in morphology, physiology, biochemistry, ecology, pathology, or sexual compatibility system. Computer-aided comparative studies of such attributes could assist research into species relatedness.

Divergent nucleic acid composition has probable utility in ascertaining species relatedness. Anderson and others (1987) concluded that some particular DNA sequences may be appropriately variable for phylogenetic studies. Subsequently, Anderson and others (1989) showed that some European *Armillaria* species and the equivalent or unidentified North American Biological Species, or NABS, (Anderson and Ullrich 1979; Bérubé and Dessureault 1988, 1989) could be placed in distinct classes based on restriction maps of ribosomal DNA. These are: rDNA class 1, *A. ostoyae* (= NABS I); class 2, *A. gemina* (= NABS II); class 3, *A. borealis*; class 4, *A. sinapina* (= NABS V); NABS IX, X; class 5, *A. calvescens* (= NABS III), *A. gallica* (= NABS VII), *A. cepistipes* (= NABS XI?); class 6, *A. mellea* (= NABS VI). The classes are believed, with the possible exception of rDNA class 4, to represent natural groupings. In addition, classes 1, 2, and 3 were considered to be closely related with rDNA classes 2 and 3 derived from the more widely distributed DNA class 1. Greater resolution through detailed mapping of particular regions of the genome will assist phylogeny development. As Anderson and others (1989) have suggested, reconsidering ecological, morphological, and distributional data for taxa on the basis of restriction polymorphisms would be informative.

Present and Excluded Species of *Armillaria*

Singer (1978) prepared a key to the world taxa (as *Armillariella*) he considered distinct. This key needs to be updated in light of the new taxa recognized and concepts developed since that time. Table 1.1 lists 36 taxa which we believe have been documented suffi-

TABLE 1.1 — The current nomenclature and geographical occurrence of 36 *Armillaria* species (some as *Armillariella*). The citation for the original description of each species is given. *Italic* numbers indicate those identified as both morphological and biological species.

1. *A. mellea* (Vahl:Fr.) Kummer (= Korhonen D., Anderson and Ullrich NABS VI). Europe, North America, North Asia, Japan, Africa? (type species)+.

2. *Armillariella affinis* Singer. Central America. In *Fieldiana* (Bot.).21:12 (1989).

3. *A. borealis* Marxmüller & Korhonen (= Korhonen A.). Northern Europe, Russia. In *Bull. Soc. Mycol. Fr.* 98:122 (1982).

4. *A. calvescens* Bérubé & Dessureault (= Anderson and Ullrich NABS III). North America. In *Mycologia*. 81:220 (1989).

5. *A. cepistipes* Velenovsky (= Korhonen B., Anderson and Ullrich (Morrison) NABS XI?). Europe, North America?, Japan. In *Ceske Houby*. 1:283 (1920).

6. *A. fellea* (Hongo) Kile & Watling. New Guinea. In *Rep. Tottori Mycol. Inst.* 14:97 (1976).

7. *A. fuscipes* Petch (= *A. heimii* Pegler and *A. elegans* Heim). East and West Africa, Sri Lanka, Madagascar. In *Ann. Roy. Bot. Gdn., Peradeniya*. 4:299 (1909). †

8. *A. gallica* Marxmüller & Romagnesi (= *A. lutea* Gillet sensu Arnolds and Temorshuizen, and Watling; *A. bulbosa* (Barla) Kile and Watling; Korhonen E., Anderson and Ullrich NABS VII). Europe, North America, Japan. In *Bull. Soc. Mycol. Fr.* 103:152 (1987).#

9. *A. gemina* Bérubé & Dessureault (= Anderson and Ullrich NABS II). North America. In *Mycologia*. 81:217 (1989).

10. *Armillariella griseomellea* Singer. South America. In *Beih. Nova Hedw.* 29:40 (1969).

11. *A. hinnulea* Kile & Watling. South-eastern Australia. In *Trans. Brit. Mycol. Soc.* 81:131 (1983).

12. *A. limonea* (Stevenson) Boesewinkel. New Zealand. In *Kew. Bull.* 19:13 (1964).

13. *A. luteobubalina* Watling & Kile. Australia. In *Trans. Brit. Mycol. Soc.* 71:79 (1978).

14. *A. mellea* var. *camurenensis* Henning. West Africa. In *Engl. Bot. Jahrb.* 22:107 (1895).

15. *A. melleorubens* (Berkeley & Curtis) Saccardo. Caribbean. In *J. Linn. Soc.* 10:283 (1869).

16. *A. macrospora* Peck. North America. In *Bull. Torrey Bot. Club.* 27: 610 (1900).

17. *A. montagnei* (Singer) Herink. South America. In *Lloydia*. 19:182 (1956).

18. *A. nigrītula* Orton. Great Britain. In *Notes Roy. Bot. Gdn., Edinb.* 38:316 (1980).

19. *A. novae-zelandiae* (Stevenson) Herink. New Zealand, Eastern Australia, New Guinea, South America? In *Kew Bull.* 19:14 (1964).

20. *A. olivacea* (Rick.) Herink. South America. In *Lloydia*. 19:180 (1956).

21. *A. omniūens* (Berkeley) Saccardo. India. In *Hooker's J. Bot.* 2:46 (1850).

22. *A. ostoyae* (Romagnesi) Herink (= *A. polymyces* (Secr.) Sing. & Clem; *A. obscura* Schaeff.:Fr., *A. montagnei* var *umbrinolūtea* Singer, = Korhonen C; Anderson and Ullrich NABS I). Europe, North America, Japan. In *Bull. Soc. Mycol. Fr.* 86:265 (1970).

23. *A. pallidula* Kile & Watling. Queensland. In *Trans. Brit. Mycol. Soc.* 91:307 (1988).

24. *A. praecox* Velenovsky. Central Europe. In *Ceske Houby*. 1:282 (1920).

25. *A. procera* Speggazzini. South America. In *Bol. Acad. Nac. Cienc.Cordoba*. 11:385 (1889).

26. *A. puiggarii* Speggazzini. South America. In *Bol. Acad. Nac. Cienc. Cordoba*. 11:384 (1889).

27. *A. saviczii* (Singer) Herink. Byelorussia. In *Nat. Syst. Sect. Crypt. Inst. Bot. Acad. Sci. URSS*. 4(10-12):6 (1938).

28. *A. sinapina* Bérubé & Dessureault (= Anderson and Ullrich NABS V). North America. In *Can. J. Bot.* 66:2030 (1988).**

29. *A. solidipes* Peck. North America. In *Bull. Torrey Bot. Club.* 27:611 (1900).

30. *A. sparrei* Singer (Herink). South America. In *Lloydia*. 19:183 (1956).

31. *Armillariella tigrensīs* (Singer) Raith. South America. In *Flora Neotropica Monogr.* 3:8 (1970).

32. *A. yungensis* (Singer) Herink. South America. In *Flora Neotropica Monogr.* 3:12 (1970). Subgenus *Desarmillaria*

33. *A. ectypa* (Fr.) Lamoure. Europe. In *Syst. Mycol.* 1:108 (1821).

34. *A. nigropunctata* (Secretan) Herink. Europe. In *Mycogr. Suisse*. 2: 1046 (1833).

35. *A. socialis* (DC.:Fr.) Herink. (= *A. tabescens* (Scop.:Fr.) Emel.). Europe, USA? In *Syst. Mycol.* 1:251 (1821).*

36. *Armillariella watsonii* (Murrill) Singer. North America. In *Proc. FL. Acad. Sci.* 7:111 (1944)

+ For species 1,3,4,5,8,9,22, and 28, the secondary designations given are those used for the equivalent biological species by Korhonen (1978), Anderson and Ullrich (1979), and Morrison and others (1985).

† Synonymy proposed by Kile and Watling (1988) on morphological criteria, although interfertility studies are required for confirmation.

** *A. sinapina* (NABS V) may be synonymous with *A. cepistipes* (Anderson and others 1980, Guillaumin and others 1989a) but comparisons of basidiome morphology and further interfertility studies between European and North American material are necessary to resolve this question.

The binomial *A. gallica* is preferred as its identity is unequivocal, being supported by a type specimen, a culture, a full description, and a plate.

* While the name *A. (Clitocybe) tabescens* has been frequently used for a taxon common as a pathogen in southeastern USA, it is probably a different species than that found in Europe (Guillaumin and others 1989a).

ciently to be considered species, although a few additional taxa will probably be delineated eventually. It includes all species known to be significant to plant pathologists and ecologists. Nomenclatural adjustment of some of Singer's *Armillariella* species is required. Fourteen of the species have been recognized as both morphological and biological species (see chapter 2), and future interfertility-morphological studies may result in changes to the status of other species listed in table 1.1.

Since Fries (1821), many species have been placed in *Armillaria* by virtue of possessing a white to cream-color spore-print and an annulus, which make it very heterogenous. With a more restricted generic concept for *Armillaria*, knowing where some of these taxa formerly placed within *Armillaria* are now assigned is useful. Table 1.2 shows the concordance of Fries (1821) species with modern concepts. Fries (1838, 1854, 1874) included an additional 34 species in the *Armillaria* group, only one of which was possibly an *Armillaria* species s.s. (*A. laricinus* = *A. ostoyae*?). Many velate species of *Tricholoma* have been placed in *Armillaria*, and *T. caligata* (Viv.) Rick. and its allies have been traditionally placed by North Americans in the genus (Hotson 1941, Mitchel and Smith 1976, Smith 1979, Thiers and Sundberg 1976). This is erroneous and confusing because the species are morphologically, ecologically, and biologically quite distinct from *Armillaria* species s.s.

Romagnesi (1970, 1973), Termorshuizen and Arnolds (1987), Watling (1987), and Watling and others (1982) discussed the identity of *Armillaria* species illustrated in the classical literature.

TABLE 1.2 — Concordance of Fries' Systema Mycologicum (1821) species in Agaricus Tribe III *Armillaria* with modern concepts.

Species	Family
1. <i>A. robustus</i> = <i>Tricholoma</i>	Tricholomataceae
2. <i>A. persoonii</i> *	
3. <i>A. guttatus</i> = <i>Limacella</i>	Amanitaceae
4. <i>A. bulbiger</i> = <i>Leucocortinarius</i>	Cortinariaceae
5. <i>A. constrictus</i> = <i>Calocybe</i>	Tricholomataceae
6. <i>A. subcavus</i> = <i>Limacella</i>	Amanitaceae
7. <i>A. mucidus</i> = <i>Oudemansiella</i>	Tricholomataceae
8. <i>A. vagans</i> *	
9. <i>A. griseofuscus</i> *	
10. <i>A. denigratus</i> = <i>Agrocybe erebia</i>	Bolbitiaceae
11. <i>A. rhagodiosus</i> = <i>Lentinus lepideus</i>	Pleurotaceae
<i>A. melleus</i>	

* *A. vagans*, and *A. griseofuscus* cannot be equated with *A. robustus* and are best considered *nomen dubium*.

Recent major contributions to the description of morphological variation and the delineation of *Armillaria* taxa include those of Romagnesi (1970, 1973, 1978); Marxmüller (1982, 1987); Marxmüller and Printz (1982); Romagnesi and Marxmüller (1983); Watling (1987) for Europe; Singer (1956, 1969) for South America; Stevenson (1964) and Kile and Watling (1981, 1983, 1988) for Australasia; and Bérubé and Dessureault (1988, 1989) for North America. Although Chandra and Watling (1982) redescribed several Indian species, fresh collections are required to complement their herbarium studies. Mohammed and others (1989) and Mwangi and others (1989) reported cultural, genetic, and isozyme studies of African species which will help to resolve their identity. Further research is necessary for other areas such as Siberia, China, and parts of South-east Asia.

Taxonomic Characters and Identification

As with other macromycetes, species of *Armillaria* are delimited primarily by basidiome morphology (fig. 1.2). While vegetative isolates may be identified or grouped by various methods, basidiomes are essential for the complete description and naming of species.

Basidiome macromorphology, pileipellis structure and ornamentation, ring characteristics, stipe ornamentation, presence or absence of subhymenial or basidial clamps, location of pigments in cell walls or vacuoles, and basidiospore size and ornamentation are among characters of value for species differentiation. Separation of some species by morphological criteria alone is difficult but no more so than in many other agaric genera. Identification may require using numerous macro- and micromorphological features combined with biochemical, cultural, and ecological information. A thorough appreciation of the most useful taxonomic characters will only be derived from careful analyses of all these features (Watling and others 1982).

Analysis of European, and to a lesser extent Australasian species (Kile and Watling 1983, Shaw and others 1981), showed that it is possible to identify some species by morphological and physiological attributes of their vegetative mycelia and rhizomorphs as well as by basidiome morphology (table 1.3). Additional simple tests such as the response of the mycelium to light may also differentiate some species (Benjamin 1983; see also Hood and Sandberg 1987).

Serological differences among several *Armillaria* species were demonstrated by Lung-Escarmant and others (1978, 1985b) and Lung-Escarmant and Dunez (1979, 1980); serological techniques may, in the future, have a substantial impact on the delimitation of *Armillaria*



FIGURE 1.2 — Basidiomes of 12 *Armillaria* species from various regions of the world, demonstrating variation in the macromorphology of basidiomes. A: *A. ostoyae*; B: *A. limonea*; C: *A. novae-zelandiae*; D: *A. pallidula*; E: *A. mellea*; F: *A. fumosa*; G: *A. calvescens*; H: *A. luteobubalina*; I: *A. gallica*; J: *A. sinapina*; K: *A. tabescens*; L: *A. ostoyae* produced in vitro. (G.A. Kile, H. Burdsall, A. Lynch, J. Worrall, P. Wargo, C.G. Shaw III, T. Harrington)

TABLE 1.3 — Morphological, physiological, and serological differences among *Armillaria* species common in Europe (*A. mellea*, *A. borealis*, *A. cepistipes*, *A. gallica*, *A. socialis*, and *A. ostoyae*).*

	Differences between species	References
1. Morphology of basidiomes in nature	All species different Difficult distinction between <i>A. gallica</i> and <i>A. cepistipes</i>	Romagnesi 1970, 1973 Marxmüller 1982, 1987 Romagnesi and Marxmüller 1983 Roll-Hansen 1985 Motta and Korhonen 1986 Watling 1987 Intini 1988
2. Morphology of basidiomes in vitro	Useful for <i>A. ostoyae</i> , <i>A. borealis</i> and <i>A. cepistipes</i>	Guillaumin 1986a
3. Morphology of the mycelium in pure culture	All species different except <i>A. gallica</i> and <i>A. cepistipes</i>	Korhonen 1978 Guillaumin and Berthelay 1981 Rishbeth 1986 Mohammed 1987 Intini and Gabucci 1987 Guillaumin and others 1989a
4. Morphology of subterranean rhizomorphs in nature	<i>A. ostoyae</i> , <i>A. mellea</i> and <i>A. gallica</i> different	Morrison 1982
5. Morphology of subterranean rhizomorphs in a mist box	All species different except <i>A. gallica</i> and <i>A. cepistipes</i>	Mohammed 1985, 1987 Guillaumin and others 1989a
6. Response to temperature	Different temperature optima. Poor growth of <i>A. mellea</i> but good growth of <i>A. socialis</i> at 30 degrees C	Rishbeth 1986 Mohammed 1987
7. Reaction to phenolic acids and terpenes	Specific reaction of <i>A. gallica</i> , others quite variable	Shaw 1985 Rishbeth 1986 Mohammed 1987 Guillaumin and others 1989a
8. Polyclonal antibodies	Separate <i>A. mellea</i> , <i>A. gallica</i> , <i>A. ostoyae</i> , <i>A. socialis</i>	Lung-Escarmant and Dunez 1979, 1980 Lung-Escarmant and others 1978, 1985

*Modified from Guillaumin

species. Fox and Hahne (1989) used monoclonal antibodies, but the results to date are not as impressive as those obtained by studies using polyclonal antibodies. Refinement of the techniques by developing greater antibody specificity to overcome problems of cross reactivity between closely related species may allow accurate identification in the near future, including the possibility of diagnostic kits for rapidly identifying field material.

Analysis supports current species concepts and offers a powerful diagnostic tool. (1986) reported quantitative differences in DNA content between *A. mellea* and *A.*

gallica. Jahnke and others (1987) and Anderson and others (1987, 1989) showed that mitochondrial (mt) DNA was highly conserved within species but divergent between them, and that restriction fragment patterns were therefore diagnostic for species. Smith and Anderson (1989) correctly identified 23 North American isolates using DNA restriction fragment length polymorphisms.

Isoenzyme and protein profiles of some northern hemisphere taxa also differ sufficiently to offer further methods of species separation (Lin and others 1989, Lung-Escarmant and others 1985b, Morrison and others 1984).

The biological species concept has been applied to the genus using single basidiospore isolates to delineate reproductively isolated groups as discussed in chapter 2. Using this particular approach has greatly assisted taxonomists in defining species in genera with restricted interspecific but high intraspecific morphological variation. Reproductively isolated groups have been linked to existing taxa (Marxmüller 1982, Romagnesi and Marxmüller 1983), led to the description of new taxa (Bérubé and Dessureault 1988, 1989; Marxmüller and Korhonen in Marxmüller 1982; Marxmüller 1987), and established intra- (Anderson and Ullrich 1979, Kile and others 1983, Korhonen 1978) and inter-continental distributions (Anderson and others 1980, Guillaumin and others 1989a, Morrison and others 1985a). Conversely, species initially described on conventional criteria were later shown to be biological species (Guillaumin 1986a, Kile and Watling 1988).

Cumulative experience suggests that reconciling morphological (taxonomic) and biological species concepts for most *Armillariae* will be possible. Although such studies will take time to complete, they should result in robust characterization of species. In cases for which detailed morphological examination supports a single species but interfertility studies indicate otherwise, Watling and others (1982) suggested adopting the macro-microspecies concept in which a macrospecies would consist of morphologically indistinguishable biological species. We support this suggestion.

Conclusions

Major studies of *Armillaria* taxonomy have been completed in recent years. Linking morphological, cultural, physiological, and genetic data has often

enhanced their individual values; the frequent concordance of information from a variety of sources has more clearly defined many taxa. Additional collections and application of various techniques to assess phenotypic and genotypic variation within the *Armillaria* flora in regions where it is incompletely known remain necessary to enhance our taxonomic understanding of the genus on a worldwide basis. Analysis of collections on which some early names are based will further assist the quest for nomenclatural stability within the genus.

The genetic approach to species differentiation, initiated for *Armillaria* by Korhonen (1978), allowed the identification of species from vegetative isolates. Subsequent work has shown that vegetative isolates also may be distinguished by other cultural or physiological characteristics. The ability to identify vegetative isolates is highly useful for organisms in which the vegetative phase may often be the only one encountered. Newer techniques such as DNA analysis and production of monoclonal antibodies have the potential to further enhance rapid and reliable identification of vegetative isolates.

The morphological and biological species concepts appear largely reconcilable for *Armillaria*, at least on the basis of our knowledge of temperate species. This perhaps fortuitous situation will continue to have a marked impact in clarifying the taxonomy of the genus.

A stable nomenclature, well-defined species, and a variety of identification techniques are invaluable to pathologists and ecologists in their attempts to understand the behavior and natural relationships of *Armillaria* species, clarify their natural relationships, and develop disease-control strategies. Progress has been significant in the former areas in recent years.

Life Cycle, Interfertility, and Biological Species

Jean-Jacques Guillaumin, James B. Anderson, and Kari Korhonen

Species are traditionally identified by their morphological characteristics. Within the last few decades, however, the “biological species” concept has assumed an increasingly important role in mycology. A biological species is a group of “individuals” sharing a common gene pool. In the field, there is little or no genetic exchange between biological species (Esser and Hoffman 1977). Although the biological species is a rather limited concept dependent only on the criterion of interbreeding, it has already had a major impact on formal taxonomy. Among basidiomycetes especially, interfertility tests very often conclusively indicate species identity (Boidin 1977, Boidin and Lanquetin 1984). Of course, interfertility tests can only be conducted with sufficient knowledge of the sexual incompatibility systems and life cycles of the fungal group under investigation. In the genus *Armillaria*, interfertility tests became possible only when the riddle of sexuality was solved, beginning with Hintikka in 1973.

In the Basidiomycetes, single basidiospores germinate to produce a mycelium usually consisting of haploid, monokaryotic (uninucleate) cells. In heterothallic species, haploid monokaryons anastomose with one another upon contact; if they are sexually compatible, a fertile mycelium usually consisting of dikaryotic (binucleate) cells results. In many, but not all, species, the synchronous division of the paired nuclei in a dikaryon accompanies the formation of clamp connections, the presence or absence of which is the most widely used criterion for judging whether a pairing of haploid monokaryons is sexually compatible or incompatible.

The dikaryon predominates in the vegetative phase of most basidiomycetes. During vegetative growth, the component nuclei remain paired but do not fuse. In the basidia does nuclear fusion (karyogamy) immediately before meiosis and the formation of basidiospores (fig. 2.1).

Most basidiomycetes are heterothallic. The haploid monokaryon is self-sterile, and a dikaryon appears only when two haploid monokaryons carrying different alleles at the mating-type locus or loci contact one another and mate. “Unifactorial” species have one mating-type locus, and the monospore isolates from a single basidiome segregate as two classes or “mating types” (“bipolar pattern of sexuality”). “Bifactorial” species have two mating-type loci, and the monospore isolates from a basidiome segregate as four mating-types (“tetrapolar pattern of sexuality”).

A few basidiomycetes are homothallic. The haploid monokaryon is self-fertile, and becomes dikaryotic and fertile even without mating with another strain. “Pseudohomothallic” species have a uni- or bifactorial sexual incompatibility system, but individual basidiospores may receive two postmeiotic nuclei carrying

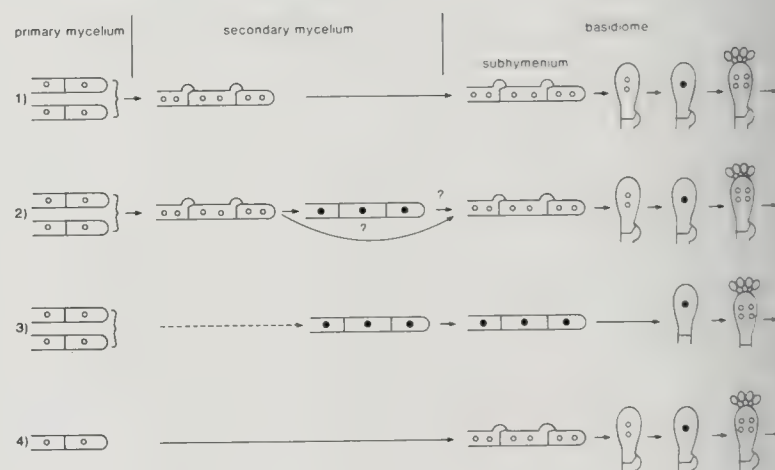


FIGURE 2.1 — Caryological cycles: 1) a typical hymenomycete with dikaryotic secondary stage; 2) a heterothallic *Armillaria* with dikaryotic subhymenium; 3) a heterothallic *Armillaria* with diploid subhymenium; 4) a homothallic *Armillaria* (*A. ectypa*; there are also homothallic *Armillaria* species with monokaryotic subhymenium). Open circles are haploid nuclei, dark circles diploid. The cycles of *Armillaria* are somewhat hypothetical.

compatible mating types. The resulting monospore isolates of these species are self-fertile but for a different reason than in true homothallic species.

Some early researchers (Kniep 1911, Kühner 1946) observed that *Armillaria* did not fit the general concept of the higher basidiomycete life cycle. They noted the hyphal cells of *Armillaria* are monokaryotic, irrespective of whether the culture originates from a single basidiospore, basidiome tissue, or vegetative material from the field. One plausible explanation was that *Armillaria* is homothallic. An observation inconsistent with homothallism and inbreeding, however, was that monospore mycelia originating from a single basidiome vary considerably, suggesting meiosis and recombination in a heterozygous parent (Raabe 1953, Snider 1957). The state of knowledge of the *Armillaria* life cycle was aptly summarized by Raper (1966): "All criteria point to an asexual or homothallic pattern of development, save one: the variability among the monosporous progeny of single fruiting bodies."

The Sexual System

Mating Reactions Among Haploids

Hintikka (1973) made the first and most important contribution to solving the problem of sexual reproduction in *Armillaria*. He observed a macromorphological difference between monospore and tissue cultures of *Armillaria*. The monospore isolates usually produce a white or light-brown aerial mycelium which gives the colony a fluffy appearance. Cultures from basidiome tissues, however, are flat, crustose, and lack aerial mycelia. Based on this morphological distinction, Hintikka showed that *Armillaria* had a bifactorial sexual incompatibility system. When sibling monospore isolates were confronted in culture, the colony morphology of certain pairwise combinations changed from the fluffy to the flat and crustose appearance. Also, because the cells both of unmated monospore isolates and of basidiome tissues are monokaryotic, he suspected that the nuclei in crustose mycelia were diploid. Diploidization in matings was proved later by several different lines of investigation.

According to the bifactorial sexual incompatibility system, each haploid mycelium of *Armillaria* contains two mating-type alleles, A_x and B_x . After two haploid mycelia (belonging to the same species) contact one another and anastomose, one of four possible events may occur (fig. 2.2):

(1) **Incompatible mating** [$A_1B_1 \times A_1B_1$]: The haploid partners grow side by side without intermingling,

and without any substantial changes in macro- or micromorphology.

(2) **Compatible mating** [$A_1B_1 \times A_2B_2$]: The partners intermingle eventually to form a homogeneous colony while the morphology changes from the fluffy to the flat, crustose type. Partially disintegrated septa are visible in some hyphae, indicating nuclear migration. Most species also have some dikaryotic hyphae with clamp connections. Nuclear migration and diploidization proceed rather slowly in matings of *Armillaria*, only about 2-3 times faster than the growth of hyphae (Korhonen 1983).

(3) and (4) **Hemicompatible common-A and common-B matings** [$A_1B_1 \times A_1B_2$ and $A_1B_1 \times A_2B_1$]: One of these combinations is similar to an incompatible mating, but in the other combination, a broad "barrage" zone usually develops between the partners. Aerial mycelium is sparse or lacking, and sometimes the crustose mycelial type is also seen in this zone. Some ambiguity persists about the assignment of A and B factors, however. According to one interpretation, the latter hemicompatible interaction is common-A because signs of nuclear migration (disintegrated septa) can be found in some hyphae of the barrage zone, suggesting the presence of different- B alleles (Korhonen 1978). According to the other interpretation, the crustose mycelium on the barrage zone is a common-B diploid (Guillaumin and others 1983).



FIGURE 2.2 — Appearance of different incompatibility factor combinations in matings of *A. ostoyae*: incompatible, two hemicompatible, and compatible matings (from upper left to lower right). Age of cultures: 6 weeks. (J. Anderson)

When single-spore isolates from one basidiome are paired with each other, these four mating factor combinations appear at about equal frequencies. The great majority of pairings within a large population are compatible because the number of different alleles in the population is large, and because in any given pairing of nonsiblings collected from different localities their alleles are unlikely to be identical. No reliable estimates gauge the total number of different mating-factor alleles in the species of *Armillaria*. As judged on the basis of some large mating tests, the number must be several dozen at least. In this respect, *Armillaria* is similar to other bifactorially heterothallic basidiomycetes.

The existence of the same bifactorial sexual incompatibility system has now been shown in all temperate *Armillaria* species (Guillaumin 1986a, Guillaumin and others 1983, Kile 1983b, Kile and Watling 1988, Korhonen 1978, Ullrich and Anderson 1978) that have been investigated, except for the very rare Eurasian species *Armillaria ectypa* (Korhonen unpubl., Guillaumin unpubl.).

Matings Between Diploids and Haploids

A process analogous to the Buller phenomenon exists in *Armillaria* (Anderson and Ullrich 1982a; Korhonen 1978, 1983). When a fluffy haploid mycelium is paired with a crustose diploid isolate of the same species, in many cases the morphology of the former progressively changes to crustose, indicating diploidization. The Buller phenomenon in its original sense (Raper 1966) is a mating between a monokaryon and a dikaryon: the dikaryon donates compatible haploid nuclei to the monokaryon, which is "dikaryotized." In *Armillaria*, the donor mycelium is diploid; the exact mechanisms of diploid-haploid mating are not known. In most cases, the diploid nuclei apparently replace the haploid nuclei in the opposing mycelium; occasionally, however, recombinant diploids appear, indicating that haploidization has taken place in the original diploids (Guillaumin 1986a).

The Caryological Cycle

Vegetative Diploidy

In a typical basidiomycete, the final result of compatible mating is a heterokaryotic mycelium with two or more haploid nuclei in each cell. In the genus *Armillaria*, the result is a diploid mycelium with uni-nucleate cells although the cells in older parts of the mycelium, in basidiomorphs, and in basidiomes, are commonly multinucleate.

When two haploid, monokaryotic cells mate, they first unite to form a dikaryotic stage with binucleate cells and clamp connections (fig. 2.1). This stage is only transient in *Armillaria*. Within a few days, the isolated dikaryotic hyphae become monokaryotic. This change is caused by somatic nuclear fusion and diploidization in the tip cells. After nuclear fusion, the cell undergoes mitotic division. This peculiar cell division produces two monokaryotic diploid cells from one dikaryotic cell (fig. 2.3). The diploid tip of the hypha continues to grow and dikaryotic cells are no longer apparent (Anderson 1982, Korhonen 1983, Korhonen and Hintikka 1974). Despite the instability of the dikaryotic hyphae, they can be cultivated by transferring dikaryotic tips repeatedly to a new medium (Korhonen and Hintikka 1974).

This mating process has been observed in several species of *Armillaria* including *A. borealis*, *A. gallica*, *A. cepistipes*, *A. ostoyae*, and *A. tabescens*. All of these species have a transient, but distinct, dikaryotic stage in compatible matings (Anderson 1982, Guillaumin 1986a, Korhonen 1978). The mating process in *A. mellea* seems to be somewhat different. A dikaryotic stage has never been found (figs. 2.1-2.3), and the diploidization mechanism in this species is unclear (Guillaumin 1986a).

Several additional lines of evidence show that the vegetative stage of *Armillaria* is diploid. In *A. ostoyae*, auxotrophic mutants with various nutritional deficiencies have been recovered from haploid, single-spore isolates and used as markers to investigate the mating

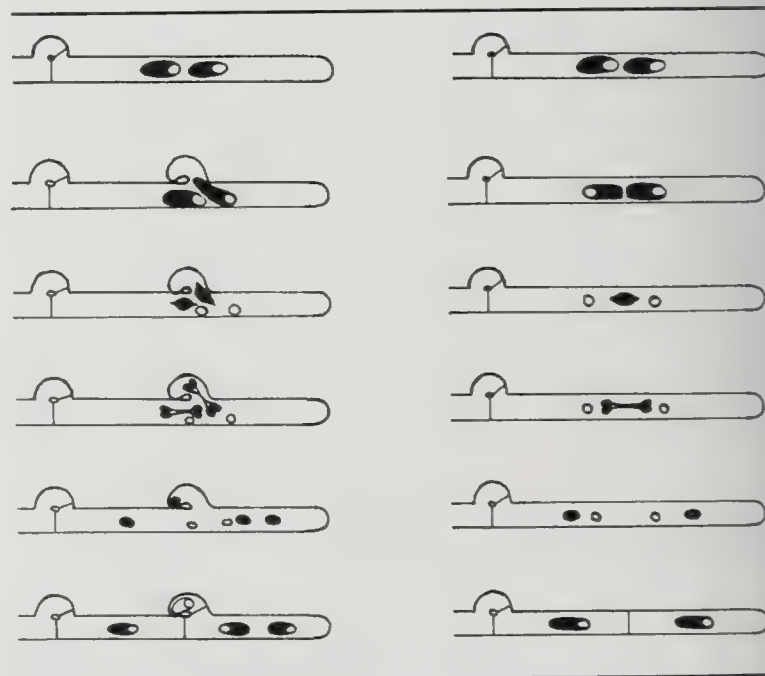


FIGURE 2.3 — Normal conjugate mitosis (left) and diploidization with subsequent mitosis (right) in a dikaryotic tip cell of *A. cepistipes*. Dark area is nucleoplasm (chromatine), open circle nucleolus (Korhonen and Hintikka 1974).

process (Ullrich and Anderson 1978). In compatible pairings of haploid strains carrying complementary auxotrophic mutations, prototrophic hyphae are recovered at a high frequency from the periphery of the mated colony. The prototrophic tips invariably consist of uninucleate cells. The observed prototrophy is due to complementarity between the haploid, auxotrophic mates within a diploid nucleus. Diploids are occasionally formed also in sexually incompatible matings, but only at low frequency and only when strong selection is applied (Anderson and Ullrich 1982a).

Diploidy has also been shown by direct measurement of individual nuclear DNA contents using fluorescence photometry of material stained with the DNA binding fluorochromes mithramycin (Franklin and others 1983) and DAPI (Peabody and Peabody 1985) as well as of Feulgen-stained material (Peabody and Peabody 1984). In these kinds of studies, the fluorescence values of individual nuclei vary greatly because the vegetative hyphae are unsynchronized with respect to cell cycle, and because the technique inherently suffers considerable measurement error. Therefore, the most meaningful tests compare the average fluorescence values of similar cell types of distinctly different ploidy levels. In mithramycin-stained material, purified diploids from matings have on average twice the mean nuclear DNA content of their component haploid strains (Franklin and others 1983). Nuclei with DNA content consistent with diploidy are also found in mated single-spore isolates (Peabody and Peabody 1985).

The most convincing evidence for diploidy involved *A. ostoyae* and sexual reproduction. A single, uninucleate, putatively diploid cell was isolated from a mating of single-spore isolates. The resulting culture formed basidiomes, and all four segregant mating types were identified among the meiotic progeny (Guillaumin 1986a, Korhonen 1980).

Besides *Armillaria*, no other hymenomycete with a diploid vegetative stage is known to occur in nature. Exceptional diploid strains of *Schizophyllum* (Koltin and Raper 1968) and *Coprinus* (Casselton 1965) have been produced in the laboratory.

Somatic Haploidization

The diploid vegetative stage of *Armillaria* has proved to be remarkably stable. For example, of 1,224 hyphal tips isolated from 17 diploids resulting from both compatible and incompatible matings of auxotrophic strains, only two expressed segregant, auxotrophic phenotypes (Anderson and Ullrich 1982a). One segregant was from an $A \neq B \neq$ diploid. It retained heterozygosity at both mating-type loci and expressed one of the two auxotrophic markers. The other segregant was from an $A \neq B =$

diploid, and was no longer heterozygous at the *A* locus and expressed both auxotrophic markers. The mechanism of low-frequency “spontaneous” segregation is not known.

Another means of obtaining somatic segregants of *Armillaria* diploids was to use various agents known to cause somatic segregation in diploids of other, higher fungi. Of benomyl, ultraviolet light, formaldehyde, and para-fluorophenylalanine, only benomyl was effective in increased somatic segregation in *Armillaria* diploids (Anderson 1983). Two different kinds of selection can be used (Anderson and Yacoob 1984). When the parent diploid is crustose, colonies arising from fragments of benomyl-treated mycelium can be scanned for the fluffy morphology. Alternatively, when the parent diploid is prototrophic and heterozygous for auxotrophic alleles, colonies can be screened for auxotrophy.

The first method involves less labor because it is a visual screen. The second method involves individual testing of colonies by transfer to minimal medium. With these methods, a range of segregants can be obtained from diploids carrying various combinations of auxotrophic and mating-type markers. Some segregants retain heterozygosity at mating-type loci while some do not, and a variety of auxotrophic requirements are expressed in the segregants. Furthermore, the segregants have a variety of mean, nuclear DNA contents ranging from near haploid to near diploid levels (Anderson and others 1985). Because many of the segregants are no longer heterozygous at mating-type loci and have near-haploid DNA contents, the genetic segregation can be assumed to occur by haploidization during which one of each homologous chromosome is lost.

Overall, the parasexual system is a workable alternative to sexual reproduction for genetic analysis. This is especially so in *Armillaria* because some species/isolates of this genus do not fruit easily in pure culture. Benomyl-induced haploidization can also be used to obtain fluffy segregants from wild-collected diploid isolates (Anderson and Yacoob 1984). Haploidization may be useful, for instance, in cases when the species identification of diploid isolates in diploid-haploid matings proves difficult (Proffer and others 1987).

Benomyl's genetic effect on *Armillaria* diploids raises the possibility that the benomyl in isolation media (Maloy 1974) might alter the *Armillaria* cultures recovered. Since the concentrations of benomyl used to inhibit common contaminant ascomycetes (Edgington and others 1971) are much lower than that required to destabilize diploids of *Armillaria* (Anderson 1983), however, we believe that low concentrations of benomyl can be safely included in media used to isolate *Armillaria*.

A Possible Haploid Stage in Basidiomes

A perhaps even more curious phenomenon than vegetative diploidy is the reappearance of the haploid stage in the basidiomes of most *Armillaria* species. As had already been shown by Romagnesi (1970), the subhymenial cells and the basidia of these species are clamped. Korhonen (1980) confirmed that these clamped cells are dikaryotic, and the cytophotometric studies of Peabody and Peabody (1985) showed that these paired nuclei have DNA contents consistent with haploidy. Korhonen and Hintikka (1974) obtained pure cultures of dikaryotic hyphae from young macerated gills. The dikaryotic cultures are unstable and rapidly change into monokaryotic diploid hyphae, just as do the dikaryotic hyphae from compatible matings. This characteristic differs among the *Armillaria* species. Among the European species, *A. borealis*, *A. cepistipes*, *A. ostoyae*, *A. gallica*, and *A. tabescens*, all have clamped dikaryotic basidia, whereas the basidia of *A. mellea* develop from diploid cells and are clampless (Guillaumin 1986a). As stated above, the dikaryotic stage is also not found in the compatible matings of *A. mellea*.

Concerning the non-European *Armillaria* species, Motta and Korhonen (1986) showed that the basidiomes of NABS VI are clampless (as are those of the corresponding European species *A. mellea*) while the basidiomes of NABS VII have clamped basidia, like *A. gallica*. According to Bérubé and Dessureault (1988, 1989), the American species *A. sinapina* (NABS V), *A. gemina* (NABS II), and *A. calvescens* (NABS III) all possess clamped basidia. In contrast, the five Australasian species *A. luteobubalina*, *A. novae-zelandiae*, *A. hinnulea*, *A. fumosa*, and *A. pallidula* have clampless basidia (Kile and Watling 1983, Podger and others 1978).

As *A. ostoyae* produces basidiomes easily in vitro, the hymenium cytology of the basidiomes obtained in pure culture could be observed by Korhonen (1980) and Guillaumin (1986a). Korhonen noticed that the basidia of *A. ostoyae* in pure culture were clampless and uninucleate (like the basidia of *A. mellea* in nature). Guillaumin (1986a) found that while a majority of basidiomes of *A. ostoyae* produced in vitro had clampless basidia, some did not. Even the same isolate sometimes yielded basidiomes with either clamped or clampless basidia, suggesting that the determining factor is environmental rather than genetic. The specific conditions determining the occurrence of clamped or clampless basidia, however, have not yet been identified.

The origin of dikaryotic elements in the basidiomes of *Armillaria* is as yet unclear. Tommerup and Broadbent (1975) observed that while the stipe cells are

monokaryotic, dikaryotic hyphae arise from multinucleate cells near the developing gill folds of basidiome primordia. These authors also observed that the size of individual nuclei in the monokaryotic cells at the basidiome is about twice that in dikaryotic cells. These observations suggest that monokaryotic stipe cells, are diploid and that a nonmeiotic haploidization occurs in the basidiome trama which gives rise to haploid nuclei in the multinucleate cells and dikaryons of the gills. More recently, Peabody and Peabody (1985, 1987) reported that the monokaryotic cells of the stipe have a mean nuclear DNA content consistent with haploidy. The possible haploidization may thus occur at a stage earlier than proposed by Tommerup and Broadbent (1975).

While the nonmeiotic chromosome reduction presents an intriguing possibility, no precedent exists in other, higher fungi for such a regular, nonmeiotic reduction division occurring either within the basidiome or before basidiome initiation. Furthermore, because of the problems inherent in comparing the nuclear DNA contents of very different cell types, alternative explanations for the results of Peabody and Peabody (1985, 1987) are possible. First, one cannot assume that each individual cell contains a full DNA complement and that no DNA degradation occurred if the stipe cells are not known to be viable. Second, and perhaps less likely, the degree of DNA staining or of fluorescence quenching may depend on the specific cell type. These and other factors might produce a lower than expected average fluorescent yield for stipe cells as compared with other stages.

Whether the possible nonmeiotic haploidization occurs in the trama of the basidiome or at a stage preceding the basidiome formation, it would be expected to produce a mosaic of haploid strains including all four mating types from any diploid strain. If the stipe consists of a mixture of haploids, then, why do cultures isolated from the stipe invariably appear as typically crustose diploids? Arguably, mating may occur among haploid components of the basidiome isolated on artificial medium, but it should be possible to recover the haploid components by maceration or micromanipulation. To our knowledge, this has not been reported.

An alternative explanation for the origin of the subhymenial dikaryon is that no "extra" nonmeiotic haploidization occurs in the life cycle of *Armillaria* species, but that vegetative haploids may exist in the field along with diploids and may participate in the basidiome formation. Even if vegetative "germ-line" haploids do occur in the field, something must explain why cultures from vegetative material in the field usually appear crustose and diploid. Here, too, it could be argued that mating occurs among the haploid components

when the material is isolated into pure culture. If this is the case, then it should be possible to recover the vegetative haploids by maceration or micromanipulation.

Nuclear Behavior in the Hymenium

The behavior of basidium nuclei in *Armillaria* species has recently been investigated by Chahsavan-Behboudi (1974), Peabody and Motta (1979), Nguyen (1980), and Guillaumin (1986a). Two haploid nuclei enter the basidium of those species having a dikaryotic subhymenium, and one diploid nucleus enters the basidium of those species with a monokaryotic subhymenium. From this point, the overall pattern of meiosis and basidiospore formation appears to be similar to other hymenomycetes. The four nuclei resulting from meiosis migrate to four spores formed on the basidium. Various anomalies are frequently observed, however. Additional mitotic divisions may occur in the basidium, resulting in more than four nuclei. Only four nuclei, however, move to the top of the basidia and enter the developing basidiospores; the other nuclei degenerate. Also, the number of sterigmata can be two, three, or five instead of the usual four. A small number of basidiospores (1%-5%) are binucleate (Guillaumin 1986a). Observations of the basidia of *A. gallica*, *A. mellea*, and *A. ostoyae* suggest that the haploid chromosome number (*n*) in these species is four (Guillaumin 1986a, Nguyen 1980).

Identification and Occurrence of Biological Species

Identification

Since Korhonen (1978) and Anderson and Ullrich (1979), interfertility tests have become a common method for routine identification of species and for differentiation of unknown isolates into groups. Mating tests are performed using haploid tester strains (monospore isolates) that represent each species to which the isolate could possibly belong. The unknown isolate is paired with all the tester strains, and the mating reactions scored according to the appearance of the mycelium. The unmated haploid cultures are generally fluffy, and diploid cultures crustose. However, considerable variation may occur in colony morphology depending on the species, isolate, and culture conditions. Haploid cultures are sometimes rather crustose (especially in *A. gallica* and *A. cepistipes*); conversely, diploid cultures may be relatively fluffy, (especially in *A. mellea*). Furthermore, a diploid culture of some species often grows submerged in the agar medium without crustose mycelium (and aerial hyphae). In some species (*A. gallica* and *A. cepistipes*), the submerged mycelium discolors malt extract agar medium intensely brown; in

others (*A. ostoyae*), it does not. On the other hand, the haploid isolates have a strong tendency for degeneration. Their surfaces become flat and wet, and they lose their ability for mating.

Distinguishing haploid and diploid cultures by appearance alone is not always possible. However, the distinction is usually clear-cut when the amount of aerial mycelium can be compared between pairings and unmated strains. The single best rule is that compatible matings show a reduction in the amount of aerial mycelium relative to the unmated strains, and incompatible matings show little or no reduction in aerial mycelium.

The safest identification in mating tests is obtained when single-spore isolates from the unknown specimen are used in the test (fig. 2.4). Because of the possibility that the tester and the unknown haploid culture may be conspecific but incompatible due to identical mating alleles, at least two different testers must be used for each species. The pairings are usually done on malt extract agar (1%-2%) in petri dishes. Because the diploidization process in *Armillaria* is rather slow, the

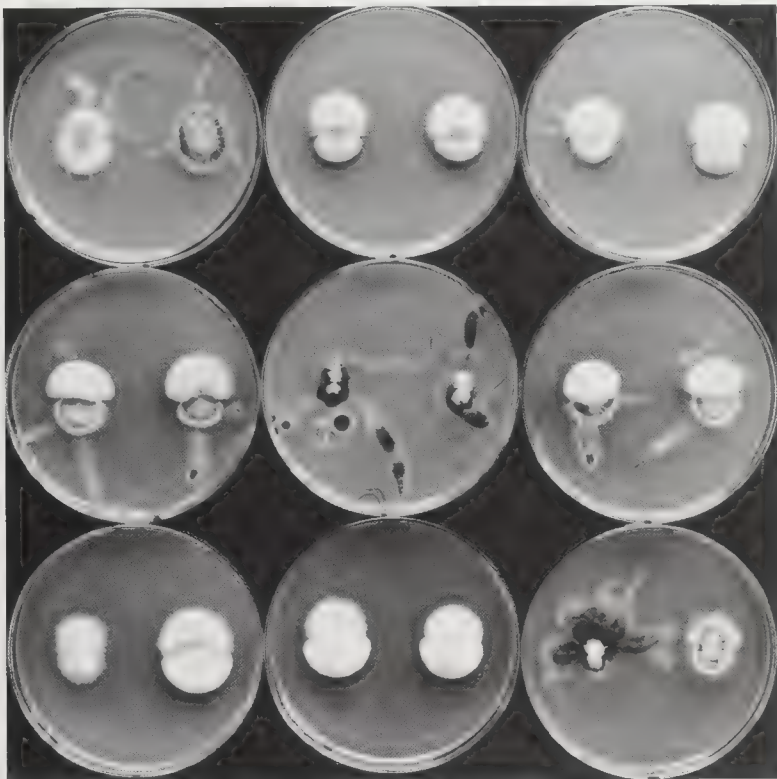


FIGURE 2.4 — Species identification of haploid isolates in a mating test. Each dish contains two pairings; in each pairing, the upper inoculum is a haploid tester strain, and the lower inoculum is the isolate to be identified. On vertical rows, there are two testers from *A. borealis* (sp. A), *A. cepistipes* (sp. B), and *A. ostoyae* (sp. C), respectively. On horizontal rows, three unknown haploid isolates have been paired with all six testers. The uppermost isolate proves to belong to *A. borealis*, the middle to *A. cepistipes*, and the lowest to *A. ostoyae*. Age of cultures: 20 days. (J. Anderson)



FIGURE 2.5 — Species identification of diploid isolates in a mating test. The arrangement is the same as in fig. 2.4, but the unknown isolates are diploid. Tester reactions like those of *A. ostoyae* (lowest right) are not uncommon; the testers show only slight inhibition in growth. (J. Anderson)

distance between the two inocula in each pairing should not exceed 3 mm. The results usually can be assessed after 3 weeks at room temperature, or earlier if the inocula are put closer to each other.

Diploid cultures can be identified in similar tests (fig. 2.5), which are analogous to the Buller phenomenon. Apparently because of diploidy, the testers' reactions in conspecific diploid-haploid pairings are usually much slower than in haploid-haploid pairings; sometimes the tester may fail to react at all. This sometimes makes the interpretation of diploid-haploid pairings difficult, and some patience is necessary for good results. According to our experience, a vast majority of diploid isolates can be safely identified in diploid-haploid pairings if six specific procedures are followed:

- (1) This identification method should be used only in geographic areas where the species composition has first been investigated in haploid-haploid pairings. The unknown isolate must belong to one of the tester species.
- (2) Use at least four haploid testers from each suspected species. The testers should be relatively fresh and not degenerate in colony morphology.
- (3) Large tests containing material from several species are better than small ones. Always include unpaired "control" cultures of the testers and

unknowns. It is also desirable to include known diploid cultures of different species in the test series for comparison.

(4) Read the results first after about 3 weeks (or earlier) and again after another 3 weeks or more.

Spread many dishes on the table and compare the behavior of the testers in different pairings, especially in pairings with known diploids. Relatively small changes in the appearance and growth of the testers may be important. Do not necessarily expect a drastic change from fluffy to crustose.

(5) In haploid-haploid matings as well as in haploid-diploid matings, "black lines" are formed in the agar between the cultures if they do not belong to the same species. These lines can often help considerably in diagnosis. They should not be confused, however, with the margin of the pseudosclerotia consisting of aggregated ("bladder-like") cells (Mallett and Hiratsuka 1986).

(6) When the identification is unsuccessful in the first test, make a second attempt using a larger selection of testers from the suspected species.

Additional criteria may also help in identifying unknown diploid isolates, especially from European species. The morphology of mycelial mats in standardized pure cultures (i.e., on malt agar in petri dishes) sufficiently characterizes the species to assist identification (Guillaumin 1986a, Guillaumin and Berthelay 1981, Intini and Gabucci 1987, Mohammed 1987, Rishbeth 1986). The main drawback of the method is that it cannot distinguish *A. gallica* from *A. cepistipes*. Although the criterion of culture morphology is less helpful for identification of haploid cultures, mating tests alone are usually sufficient in this case. Guillaumin and others (1989a) have shown that the ability to reproduce in standard culture and the morphology and pattern of subterranean rhizomorph branching obtained in a mist box can also be used for identification (see table 1.3).

European Species

For the European *Armillaria* species, a complete synthesis between the concepts of biological and taxonomic species has been made. This means that the "biological species," which can also be regarded as taxonomic species, differ by many characteristics. Seven species of *Armillaria* have been found in Europe, five annulate and two exannulate. The fertility within each species and sterility between different species seem to be complete. *Armillaria mellea*, *A. gallica*, and *A. ostoyae* have a circumboreal distribution. Outside Europe, they have been found in North America and Japan. Interfertility seems to be almost complete between European and American populations of *A. mellea* (NABS VI) and *A. gallica* (NABS VII), respectively, but is only partial be-

tween these populations of *A. ostoyae* (NABS I) (Anderson and others 1980, Guillaumin 1986a). *Armillaria tabescens* may also exist in Europe, North America, and the Far East but recent matings between the European and American forms (Guillaumin unpubl.) indicate that they are intersterile. The situation is even more complex for *A. cepistipes*, a European species that appears to be partially interfertile with two different North American biological species, NABS V and NABS X (Anderson 1986, Anderson and others 1980), plus fully interfertile with NABS XI (=group F, Morrison and others 1985a). NABS XI will likely prove to be conspecific with *A. cepistipes*. NABS V, however, sufficiently differs from *A. cepistipes* to be described as a separate species (*A. sinapina*, Bérubé and Dessureault 1988).

Because a complete correspondence between the biological species and the morphological species of Europe has been established, many other kinds of data can complement or verify the results yielded by the mating tests (see chapter 1). Among these, the morphological criteria generally play the most important role, although physiological, morphogenetic, and biochemical characteristics may also be used (see chapter 1).

North American Species

In North America, identifying *Armillaria* species currently consists of placing unknown isolates in one of nine known (annulate) biological species. All but NABS IX and NABS X are now either formally equated to European species or are described as new species (Bérubé and Dessureault 1988, 1989). Since at least three North American groups, NABS VII, VI, and I, are probably conspecific with the European species *A. gallica*, *A. mellea*, and *A. ostoyae*, respectively, many properties of the three European species are likely to be found in their American counterparts. Nevertheless, such an extrapolation requires caution until more information on North American material is available. For example, Mohammed and Guillaumin (unpubl.) have observed differences between the European species and their American counterparts in such characteristics as culture morphology or the conditions needed for sexual reproduction in vitro. Moreover, within NABS I the isolates of eastern and western origin seem to differ in their ability to form basidiomes in vitro and in their level of interfertility with European *A. ostoyae* (Mohammed and Guillaumin unpubl.). Also, Mexican isolates of NABS I (*A. ostoyae*) have formed basidiomes in culture (Shaw 1989a). At present, we have no reason to believe that each *Armillaria* species is panmictic over its entire range. Even though each species is unique overall, genetic differences probably exist among geographically separated populations.

In addition to the species mentioned above, NABS II, III, IX, and X have been reported in North America (Anderson 1986, Morrison and others 1985a, Shaw and Loopstra 1988). Bérubé and Dessureault (1989) have formally described NABS II as *A. gemina* and NABS III as *A. calvescens*. NABS IX and X await further study. The original testers for all the North American biological species were from Anderson and Ullrich (1979; see also Anderson 1986). Several authors have used these testers to identify North American isolates by haploid-haploid pairings (Bérubé and Dessureault 1988, 1989; Dumas 1988; Mallett and Hiratsuka 1988; Morrison and others 1985a,b; Motta and Korhonen 1986; Proffer and others 1987; Shaw and Loopstra 1988). A large number of testers from these studies are now available. Morrison and others (1985a) discovered a new biological species, NABS XI. As some American groups are entirely or partially compatible with some European species, Motta and Korhonen (1986) and Guillaumin and others (1989a) could also identify some American isolates through matings with European testers. Wargo (1989) and Guillaumin and others (1989a) mated diploid isolates with the haploid testers (diploid-haploid matings) with less satisfactory results. In spite of recent progress, more information is needed before the breeding relationships of all *Armillaria* species in the Northern Hemisphere are known.

Australasian Species

Five *Armillaria* species have been found in temperate and subtropical Australasia. The situation is very similar to that of Europe after the studies of Kile and Watling (1981, 1983, 1988). The identification of Australasian *Armillaria* species is based on the morphology of the basidiomes. Mating tests have also been extensively used by Kile, who selected a range of haploid testers for *A. luteobubalina*, *A. hinnulea*, *A. novae-zelandiae*, and *A. fumosa*. The vegetative morphology of these species is somewhat different and can be helpful for identification. Four species form basidiomes in pure culture (Guillaumin 1986a; Kile and Watling 1981, 1983), which can also aid identification either through observation of basidiome morphology or by obtaining haploid mycelia.

Other Regions

Morphological species have been described from Africa, India, Central and South America, and the Caribbean (see table 1.1), but little is known about their status as biological species. Mohammed and others (1989) found genetic criteria of limited value in separating African isolates. Little is known about the situation in Africa, China, and southeast Asia.

Variation Within Biological Species

Because the present species concepts in *Armillaria* are relatively new, the variation within individual species is poorly understood. Relevant knowledge is accumulating rapidly, however. Casual observations suggest that intraspecific variation occurs in rhizomorph branching pattern, basidiome and vegetative morphology, pathogenicity, and physiological and biochemical characteristics. Given the variation with these parameters, it is not surprising that polymorphism in isoenzyme profiles (Lin and others 1989, Morrison and others 1985b) and restriction fragment patterns in nuclear (Anderson and others 1987, Anderson and others 1989, Anderson and Smith 1989) and mitochondrial DNA (Jahnke and others 1987, Anderson and Smith 1989) exist in *Armillaria* species as they do in other species of plants, animals, and fungi that have been investigated (see also chapter 1).

Perhaps the most intriguing polymorphisms occur at the mating-type loci. Although the total number of mating-type alleles has not been estimated for any *Armillaria* species, the numbers of alleles in small samples of strains from local environs in North America (Ullrich and Anderson 1978, Anderson and others 1979), Finland (Korhonen 1978), France (Berthelay and Guillaumin 1985), and Australia (Kile 1983b) have been determined. In all cases the number of alleles was on the order of 10. Considerably more alleles likely exist within each respective species over its entire range.

The Identification of Genotypes

The identification of fungal individuals (genotypes, clones) and the investigation of their spread in natural substrates may reveal valuable information about the ecology of the fungus in general and about its infection biology in particular. Three methods of genotype identification have been used in *Armillaria* studies. First, the identification can be done on the basis of cultural characteristics of the isolates (Rishbeth 1978b). Second, genotypes can be identified by "somatic incompatibility," the formation of demarcation lines in confrontations. In wood, for instance, the demarcation lines border the territories of different fungal individuals (Rayner and others 1984). Somatic incompatibility has been applied for the identification of *Armillaria* genotypes in several studies (e.g., Adams 1974; Anderson and others 1979; Hood and Morrison 1984; Hood and Sandberg 1987; Kile 1983b, 1986; Korhonen 1978; Mallet and Hiratska 1985; Shaw and Roth 1976; Siepmann 1985; Thompson 1984). The method is simple: two diploid isolates are paired in a petri dish and the confron-

tation zone is observed after a few weeks. When the mycelia from a local site are genetically identical, they intermingle in a pairing to a single homogeneous colony. When mycelia from a site are genetically different, they form a permanent demarcation line between each other in a pairing. The reaction can be intensified by cultivating the fungi in wood blocks (Hood and Morrison 1984).

The test based on somatic incompatibility is a very useful method for identifying fungal genotypes. Some reservations in its usefulness are necessary, however. It has been found in experiments carried out with several species of Basidiomycetes that this method does not always distinguish between closely related heterokaryons, especially sibcomposed heterokaryons (products of compatible matings between single-spore mycelia originating from one genotype) or their parent heterokaryon (Adams and Roth 1967, Barrett and Usčuplić 1971). In *Armillaria*, the situation is comparable: sibcomposed diploids, although genetically different, produce a distinct line of demarcation in only about half the pairings (Kile 1983b, Korhonen 1978). The occurrence of sibcomposed diploids in the neighborhood of an intensively sporulating parent mycelium is possible, at least, if not likely. Furthermore, the reactions between different diploid genotypes of the same species should not be confused with reactions between diploids of different species. In the latter case, the paired mycelia usually produce a black line along the demarcation zone. The black line is usually absent in pairings between two genotypes of the same species.

The most serious reservation about the use of vegetative demarcation lines for distinguishing strains is that the genetic basis for these vegetative reactions in *Armillaria* is not known. Because the intensity of the reaction varies among genetically different diploid strains, the reaction is probably determined by many loci with allelic variation. The demarcation lines are most useful as indicators of clonal identity when they are checked against other criteria (Kile 1983b, Korhonen 1978).

The third, and least ambiguous, method used in identifying *Armillaria* genotypes is the use of mating-type alleles as genetic markers (Berthelay and Guillaumin 1985; Kile 1983b, 1986; Korhonen 1978; Ullrich and Anderson 1978). Because many *A* and *B* alleles occur in the population, it is unlikely that two outbred diploids contain identical alleles. However, sibcomposed diploids and their parent mycelium always contain identical alleles. Using mating-type alleles as markers is considerably more laborious than using demarcation reactions because haploid cultures, and often a large number of matings between them, are necessary. More sophisticated methods, such as investigation of

isozymes or other protein spectra, and especially of nucleic acids, will undoubtedly open new perspectives for studies on intraspecific variation. For example, a recent study by Smith and others (1990) showed that several clones of *A. ostoyae* (NABS I) and *A. gallica* (NABS VII) in a local area each had a unique mitochondrial genotype that was stable during vegetative growth.

The Non-Heterothallic *Armillaria* Species

The African species *A. heimii* (synonym *A. fuscipes*, table 1.1) forms basidiomes easily in pure culture (Mohammed and others 1989). Monospore isolates of this species become crustose after 10-15 days in culture. When grown on an agar medium, they are identical to each other and also to the isolate (presumably diploid) that gave rise to the basidiome. Matings among a series of different monospore isolates from the same basidiome do not show any mating reactions. It can thus be assumed that *A. heimii*, at least in the conditions of artificial culture, is not heterothallic and tetrapolar as are the European, North American, and Australian species. Additional evidence for this difference in sexuality is that some monospore isolates have given rise to basidiomes that were morphologically identical to the basidiome from which the monospore originated. Monospore isolates from these first-generation basidiomes are also crustose and identical to each other, to the parent monospore, and to the original wild isolate. Again, no mating reactions can be shown among cultures of the same series.

Such a sexual behavior can be explained either by homothallism or by parthenogenesis. Cytological observations support homothallism: the basidia are clampless, the dikaryons are lacking, and each young basidium receives a single, large (presumably diploid) nucleus. However, the sequence of the nuclear divisions in the basidium is similar to that of the heterothallic species, indicating that meiosis (and not a succession of "normal" mitoses) occurs in the basidium.

Some other tropical *Armillaria* species from Africa or the West Indies could have a similar sexual behavior, according to the preliminary results of Mohammed and others (1989). The most plausible scheme for the life cycle of these tropical *Armillaria* species would be that the basidiospores are haploid and the young germinants convert to diploidy early. The remaining parts of the cycle would be diploid. However, the nuclei of the basidiomes of these species have not yet been studied by photometry.

The non-heterothallic behavior of the tropical species could affect their dispersal. The self-fertile spores of the homothallic species do not require mates in order to complete the life cycle, and therefore may be better colonizers than those of the heterothallic species.

The quite rare *A. ectypa*, a non-tropical *Armillaria* species which grows in arctic and alpine peat bogs of Europe, might also have a non-heterothallic behavior. It forms basidiomes easily in pure culture at 18°C. The monospore cultures from such a basidiome are identical to each other and, when paired, do not exhibit any mating reaction (Guillaumin unpubl.). The same is true of the monospore cultures isolated from basidiomes of natural origin (Korhonen unpubl.). Moreover, as with *A. heimii*, some single cultures are able to form basidiomes in vitro (Guillaumin 1973). In contrast with the tropical species, however, the basidia of *A. ectypa* are clamped and dikaryotic, whether the basidiomes are of natural origin (Lamoure 1965) or originate from in vitro culture (Guillaumin 1973). Thus, the life cycle of *A. ectypa* might be homothallic with a dikaryotic stage (the homothallic equivalent of a heterothallic species with a dikaryotic subhymenium like *A. ostoyae*) while *A. heimii* would be homothallic and lacking a dikaryotic stage (the homothallic equivalent of the heterothallic species with a monokaryotic subhymenium, *A. mellea*).

Conclusions

Genetic and cytological investigations of *Armillaria* have made reliable species identification possible, and demonstrated the value of the biological species concept for the genus. Moreover, recent studies have provided new information about the caryological cycles. The mating system of *Armillaria* species is generally tetrapolar, but the genus also contains homothallic species, especially from the tropics. The caryological cycle is exceptional in that *Armillaria* is the only hymenomycete known to have a persistent and widespread diploid vegetative stage in the field. Most species have a dikaryotic stage in compatible matings, but it is short and unstable with diploidization occurring in hyphal tip cells. Although vegetative diploids are very stable, benomyl will induce somatic haploidy. A phenomenon analogous to the Buller phenomenon is found between diploid and haploid mycelia of *Armillaria*, but its underlying genetic mechanism is unclear.

Despite the predominance of diploidy in the vegetative stage, the basidiomes of most species contain dikaryotic hyphae with clamp connections; the clamped basidia arise from dikaryotic cells. The origin

of this dikaryotic stage is still unclear. The basidiomes of other species do not contain dikaryotic hyphae, and the clampless basidia arise directly from uninucleate diploid cells. The adaptive consequences of caryological variation among different species remain unknown.

Although much recent progress has been made in understanding the genetic mechanisms in *Armillaria*, we see four areas that await investigation. First, with respect to life cycles, the nature and timing of the putative non-meiotic haploidization (if indeed it occurs at all) and the mechanisms of homothallism need to be resolved. We believe that appropriate experiments can help to clarify these aspects of the *Armillaria* life cycles.

Second, because species and even individual genotypes can now be accurately identified, we can expect better resolution of epidemiological patterns, from long-range dispersal through local spread and infection in forests. Third, with sexual and parasexual crosses now available in the laboratory, it may even be possible to identify the determinants of pathogenicity. Finally, because of the considerable background on breeding relationships, morphology, ecology, and distribution of well-delineated species, *Armillaria* offers an excellent opportunity to use molecular characters to reconstruct phylogenetic relationships and to assess the relative roles of geographic isolation and intersterility in fungal speciation.

Ontogeny and Physiology

Michael O. Garraway, Aloys Hüttermann, and Philip M. Wargo

The *Armillaria* life cycle, as with other members of the Agaricaceae, involves many developmental events which lead to the expression of several morphological forms. Specific structures include fruiting bodies or basidiomes, basidiospores, mycelia, pseudosclerotial tissue, and rhizomorphs. These structures enable *Armillaria* to accommodate various habitats and allow, directly or indirectly, various species and isolates to survive in the wild and to infect and colonize diverse hosts and substrates. This adaptability strongly influences the pathogenicity of *Armillaria* (see chapter 6), and we therefore discuss these structures and their development.

Structural differentiation and development in *Armillaria* are invariably preceded and accompanied by a series of intracellular changes which redirect metabolic pathways, redistribute organelles, and rearrange structural materials. Studies which would elucidate how differentiation and development are regulated in *Armillaria* would benefit microbiologists, ecologists, plant pathologists, and others who wish to control the survival, spread, and pathogenesis of this fungus. For reasons such as these, we review the nutrition and physiology of *Armillaria*.

As a root disease fungus, *Armillaria* is one of the most prominent killers and decayers of deciduous and coniferous trees and shrubs in natural forests, plantations, orchards, and amenity plantings throughout the world. Its roles include primary pathogen, stress-induced secondary invader, and saprophyte. Yet, the physiological bases for the varied roles are not well understood. Acknowledging this limitation, we discuss the physiology of the pathogen as it relates to host-parasite interactions.

The following presentations on *Armillaria* structures and their development, nutrition and physiology, and host-parasite interactions are intended to support the discussions of biology, ecology, and pathology in other chapters.

Structure and Morphogenesis

Armillaria resembles other agaricaceous fungi in the capacity of its hyphae to differentiate into various structures. Several of these structures enable this fungus to adapt to various environmental regimes and to exploit habitats and substrates which, without the structures, would be inaccessible. The structures in consideration include: (1) basidiomes, the main generative structure (fig. 3.1); (2) mycelia (fig. 3.2); (3) melanized cells (pseudosclerotia); (4) zone lines which *Armillaria* forms after interacting with other fungi and with tissues of infected hosts; and (5) rhizomorphs (fig. 3.3).

Development of Basidiomes

Descriptions of basidiome ontogeny in agaricaceous fungi, including an *Armillaria*, were given by Hoffman (1861). Later, Hartig (1874), Beer (1911), and Atkinson (1914) studied basidiome development in material identified as *A. mellea*. The latter two authors contradicted Hartig's observation on the developmental pattern. Fischer (1909a,b) studied *Armillaria mucida*, a species now placed in *Oudemansiella* (see chapter 1).



FIGURE 3.1 — Basidiomes of *Armillaria* (probably *mellea*) at the base of a dead red oak tree. (P. Wargo)



FIGURE 3.2 A — Mycelial fans of *Armillaria* (probably *calvescens*) on the root collar of a defoliated sugar maple sapling. (From Wargo and Houston 1974)



FIGURE 3.2 B — Mycelial fans of *Armillaria* at the base of a fumigation-damaged red pine tree. (P. Wargo)

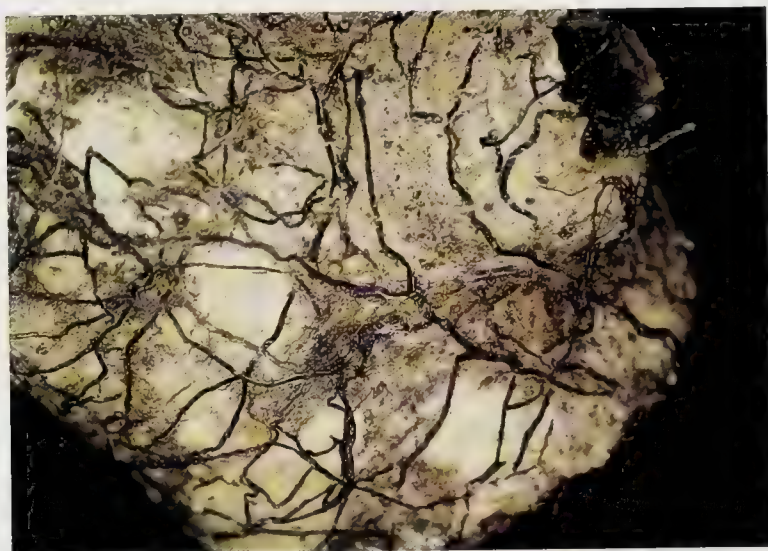


FIGURE 3.3 — Rhizomorphs of *Armillaria gallica* on a white oak root. (P. Wargo)

Reijnders (1963) and Watling (1985) classified the basidiome developmental pattern of the few *Armillaria* species so far studied as monovelangiocarpic (only a universal veil encloses the hymenial primordium) as in exannulate species, or bivelangiocarpic (when the hymenium is enclosed by a partial and a universal veil) as appears to be the case in annulate species. Some of the latter species could possibly also be metavelangiocarpic (hyphae from various tissues proliferate to grow and cover the developing hymenium), but this remains to be established. Hymenophore development is probably ruptohymenial (differentiated from the background tissue) and the overall development pattern is stipitocarpic in which the young primordium is a stipe-like group or bundle (fascicle) of hyphae lacking an apical area of differentiated cells.

A detailed morphological description of early basidiome development in *Armillaria* remains that of Atkinson (1914) for one of the North American species

(see chapters 1 and 2). While Singh and Bal (1973) studied basidiome ultrastructure in an *Armillaria* sp., further work contrasting a wider range of *Armillaria* species and using modern morphological, cytological, and biochemical methods would advance our understanding of this differentiation which is essential for the completion of the *Armillaria* life cycle.

Production of Basidiomes in Culture

Molisch (1904) first reported the formation of *Armillaria* basidiomes in culture when he grew the fungus on autoclaved bread. Falck (1907) grew *A. mellea* from basidiospores to basidiomes and reported that light was required for basidiome development (Falck 1909). That basidiomes of several *Armillaria* species may be produced in vitro has been confirmed by many subsequent studies (Bothe 1928; Falck 1930; Fox and Popoola 1990; Guillaumin and others 1984, 1985, 1989a; Jacques-Felix 1968; Kiangsu Research Group 1974; Kile and Watling 1981; Kniep 1911, 1916; Lisi 1940; Long and Marsh 1918; Mańka 1961b; Raabe 1984; Reitsma 1932; Rhoads 1925, 1945; Rykowski 1974a; Shaw and others 1981; Shaw 1989a; Siepmann 1985; Tang and Raabe 1973; Terashita and Chuman 1987). These numerous reports, however, somewhat obscure the fact that basidiome production in vitro is not yet reliably achieved, although techniques are improving. This difficulty has been noted as an important limitation to some studies (Ullrich and Anderson 1978).

Many substrates have been found suitable for basidiome development. These include bread (Falck 1930; Kniep 1911, 1916; Molisch 1904); pieces of autoclaved wood or woodchips (Guillaumin and others 1989a, Molisch 1904, Raabe 1984; Siepmann 1985, Terashita and Chuman 1987); filter paper soaked in nutrients (Reitsma 1932); oranges (Guillaumin and others 1989a,

Jacques-Felix 1968, Shaw 1989a); maize kernels (Kile and Watling 1981); nutrient solutions or agars with various amendments including fruit or plant extracts (Kiangsu Research Group 1974, Mańka 1961b, Reitsma 1932, Rhoads 1925, Rykowski 1974a, Shaw and others 1981, Tang and Raabe 1973, Terashita and Chuman 1987). Basidiomes have apparently not been produced on a synthetic culture medium. While a complex carbohydrate source appears necessary to sustain mycelial growth and basidiome development, the role of inorganic nutrients, vitamins, or other compounds in stimulating basidiome production is poorly understood. Rykowski (1974) found that the fungicide sodium pentachlorophenolate at low concentrations stimulated basidiome development, a result confirmed by Shaw and others (1981).

Incubation conditions appear to affect in vitro development of basidiomes. Kile and Watling (1981) and Raabe (1984) noted that basidiome development in cultures coincided approximately with the natural basidiome season although other authors have not observed such an association (Rykowski 1974, Shaw and others 1981, Tang and Raabe 1973). However, most success seems to have been achieved when cultures are incubated in the dark after inoculation and then exposed to fluctuating temperature/light regimes (Guillaumin and others 1984, 1985, 1989a; Kiangsu Research Group 1974; Kile and Watling 1981; Rhoads 1925; Rykowski 1974; Terashita and Chuman 1987). While Tang and Raabe (1973) claimed light was not necessary for basidiome initiation, most authors conclude that both initiation and basidiome development require light (Rykowski 1974; Guillaumin and others 1984, 1989a). In this regard, *Armillaria* resembles other agarics (Lu 1974, Niederpruem 1963, Niederpruem and others 1964). However, significant scope exists to better define the light and temperature conditions that control basidiome initiation and maturation.

Some species of *Armillaria* appear to form basidiomes more readily in culture than others (Guillaumin and others 1984, 1985, 1989a; Rhoads 1925, 1945; Shaw and others 1981; Terashita and Chuman 1987). Apart from research by Guillaumin and others (1984, 1985, 1989a) using European *Armillaria* species, little comparative study has been undertaken of the basidiome development of different species under standard conditions, although Reaves (unpubl.) has produced basidiomes of NABS I, VII, IX, and X under standard conditions. Intraspecific variation in basidiome development also requires more quantitative assessment.

Pseudosclerotial Plates and Zone Lines

Since Hartig's first description, almost every paper on wood-destroying fungi or wood decay mentions or dis-

cusses the dark lines which are characteristic for wood degraded by fungi (for general reviews, see Bavendamm 1939, Rayner and Todd 1979).

These dark lines also form in wood infected by *Armillaria*. When wood is incubated under sterile conditions with a single isolate of *Armillaria*, zone-line formation can be obtained reproducibly within 2 months (Hansson and Seifert 1987), a process which is even considered as an economically feasible method to obtain special veneers (Hansson and Seifert 1987). The compartmentalization of decayed wood in living trees, first described by Falck (1924) and further elucidated by Shigo and his co-workers (Shigo and Tippet 1981), is a completely different phenomenon and will not be discussed here.

Campbell (1934) conducted the first systematic study on zone-line formation in wood decayed by *Armillaria*. He showed that zone lines can also form in sterile wood blocks. Since then, the physiology of zone-line formation has been studied by several authors, some of whom worked with *Armillaria*. They can be produced not only in wood blocks but also in sawdust cultures (Hopp 1938) and, during intra- and interspecific pairings of different isolates, in agar culture (Mallett and Hiratsuka 1986) or wood (Hood and Morrison 1984).

Three different mechanisms appear to promote pseudosclerotial plate or zone-line formation: mechanical and physical factors, antagonistic interaction of different mycelia (incompatibility reactions), and genetic factors within a species.

Mechanical and physical factors which have been suggested to induce pseudosclerotial plate formation include:

- fluctuating moisture content (Campbell 1934, Lopez-Real and Swift 1975, Radzievskaya and Bobko 1985a);
- gas phase composition (Lopez-Real and Swift 1977);
- wounding respiration-induced damage to hyphae (Lopez-Real and Swift 1977).

Incompatible reactions between vegetative mycelia of different species or different isolates of the same species resulting in the formation of black lines have been observed frequently on decayed wood (Radzievskaya and Bobko 1985b; Rayner and Todd 1977, 1979), and during pairings of different isolates in culture (see chapter 2).

Leslie and Leonard (1979) analyzed the genetics of injury-induced fruiting in *Schizophyllum commune* Fr. and found that mechanical injury may stimulate the formation of either pseudosclerotial plates or basidiomes.

The first (serendipitous) genetic analysis of zone-line formation was performed by Holt and others (1983). During their genetic analysis of basidiome formation in *Heterobasidion annosum* (Fr.) Bref., they found that zone lines were formed only in those crosses that also formed basidiomes.

Although some conflicting results remain when different studies are compared, the formation of pseudo-sclerotial plates is, in general, a genetically determined feature of many wood-destroying basidiomycetes which is induced by various external stimuli.

The morphological changes in hyphal structure caused by zone-line induction appear to be always similar regardless of the species, the mode of induction, or the substrate on which they are formed, either inside decayed wood or in culture (Hopp 1938, Lopez-Real 1975, Mallett and Hiratsuka 1986, Rayner 1976). The process of morphogenesis of pseudosclerotia can be divided into three distinct phases (Campbell 1934, Lopez-Real 1975): proliferation of hyphae, hyphal swelling and aggregation, and pigmentation and melanization of hyphae.

The pseudosclerotial plate of *Armillaria* is thus characterized by melanized, bladder-like cells which, especially in sawdust cultures, form a brittle plate. In such cultures, infrequently two types of rhizomorphs were produced (Lopez-Real 1975). Ribbon-shaped rhizomorphs were formed in deeper parts of the culture whereas round, pigmented rhizomorphs occasionally were generated directly from the surface crust. This association between the black crust and the pigmented rind of the round rhizomorphs indicates a close similarity between these two, differentiated structures (Campbell 1934, Lopez-Real 1975).

Rhizomorphs

Rhizomorphs and mycelial cords are examples of special morphological adaptations. They are discrete, filamentous aggregations which are formed by some fungi growing on the forest floor or, as in the case of the mycelial cords of *Serpula lacrymans* Pers.:F.S. Gray, even on concrete (Thompson 1984). Rhizomorphs differ from mycelial cords in that they are highly differentiated, are fully autonomous, and grow apically; typical mycelial cords are aggregations of parallel, relatively undifferentiated hyphae. In addition, rhizomorphs grow out from a food base into substrates that may not support their growth. This feature has been described for only one fungus, *S. lacrymans* (Thompson 1984).

certain fungi to produce rhizomorphs several advantages (Thompson 1984). protection against deleterious external

agents, translocation of resources, growth from a suitable food base into an environment which initially does not support growth, enhancement of inoculum potential, and amplification of individual hyphal sensitivity to external stimuli enabling directed growth responses.

Because of their frequency in some forest soils and their wide distributions, rhizomorphs had already attracted the attention of many mycologists by the middle of the nineteenth century. Moreover, because they were somewhat self-contained units they were described by taxonomists of that time as a separate fungus species: *Rhizomorpha fragilis* Roth. This species was further divided into two subforms, *R. subterranea*, which is found within soils, and *R. subcorticalis*, which grows beneath tree bark. An early description of the different forms of *R. fragilis* was published by Schmitz (1848). He is probably the earliest investigator to describe the remarkable stability of these structures and their ability to endure prolonged desiccation after which they appear to be dead, but revive when moistened. Schmitz inferred from observing rhizomorphs in rotted timber that the fungus was probably established in the trees before felling and utilized the timber as a food base following transfer to other locations such as mine shafts. He gives an "excellent description" of *Armillaria* rhizomorphs (quoted from Hartig 1874) and their effect on standing trees.

Like most of the leading mycologists of his time, Schmitz did not fully understand the cause-and-effect relationship between the occurrence of the fungus and the disease (Ainsworth and Sussman 1965, pp. 154-156; Hüttermann 1987). De Bary (1887, pp. 28-29) gives a record of the different views on the nature of rhizomorphs which were held at that time by such outstanding mycologists as Roth, Persson, deCandolle, Eschweiler, Acharius, Fuckel, Otth, Palisoth de Beauvais, Caspary, and Tulasne.

It was Robert Hartig who resolved these differences by providing decisive proof that the rhizomorphs found in forest soils belonged to the Honey Fungus (Hallimasch), *Agaricus melleus*, now known as *Armillaria* (Hartig 1874). He carefully observed the transition between the two rhizomorphic growth forms and prepared precise illustrations of this important morphological feature of the fungus. His suggestions that different environmental conditions and differences in availability of space, in either soil or beneath the bark of living trees, influence the development and morphology of the subcortical and subterranean forms of the rhizomorphs are still valid. His early observations that browning occurs only in rhizomorphs that have been exposed to air and not in those located under tree bark have been affirmed and explained in recent work, as has his observation that the browning

process, through the formation of a dense rind, inhibits further lateral growth.

Cytology of Rhizomorphs

De Bary (1869, 1887) presents a schematic drawing of mycelial aggregation and the resulting conspicuous form of a primitive *Armillaria* thallus (fig. 3.4). A much more detailed description of rhizomorph organization is given by Hartig (1870, 1874). He clearly described the organization of the thallus (fig. 3.5) with its three layers (cortex, subcortex, and medulla); and he described and illustrated the three forms of hyphae which are characteristic of these layers. He also observed the mucilaginous nature of the rhizomorph tip and the differential formation of the cell walls in the different layers of the rhizomorph. This work was followed by that of Brefeld (1877), who first described the apical growing region as a meristem. This view of rhizomorph morphology was not improved upon until methods of tis-

sue preparation improved and electron microscopes were employed to study fungal structures. Motta (1969) examined thin sections of rhizomorph tips with the electron microscope and discerned the structure in more detail than Hartig or Brefeld were able to do (fig. 3.6). He confirmed Brefeld's earlier findings concerning

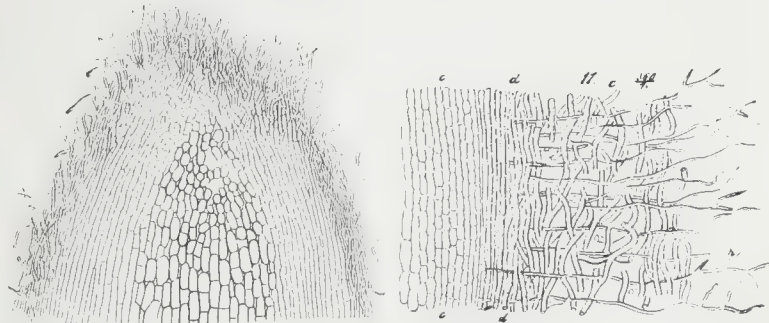


FIGURE 3.5 — Early drawing of rhizomorph (Hartig 1874).

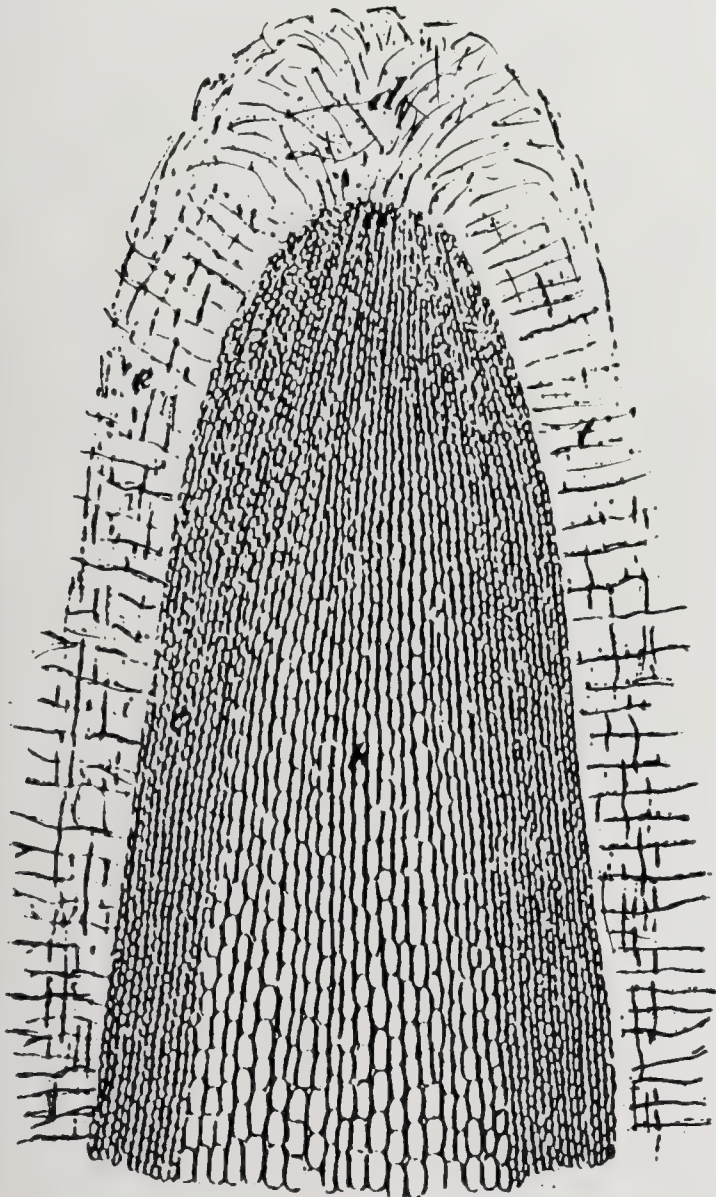


FIGURE 3.4 — Early drawing of rhizomorph (de Bary 1884).

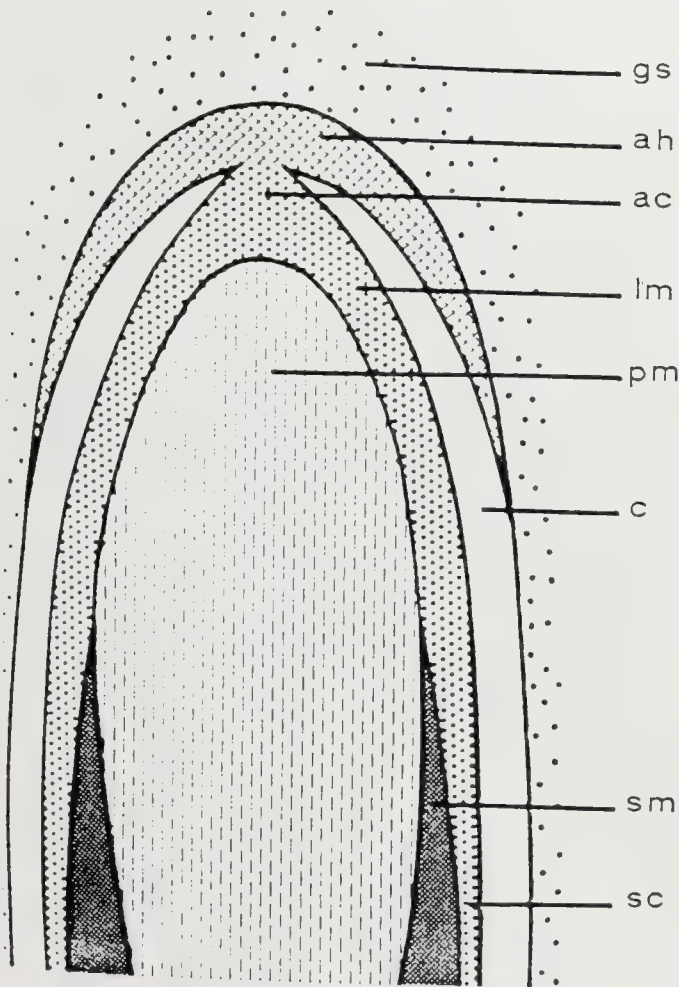


FIGURE 3.6 — Diagram of rhizomorph apex, illustrating the distribution of tissues and their origins: ah, apical hyphae; ac, apical center; lm, lateral meristem; pm, primary medulla; c, cortex; gs, gelatinous sheath; sm, secondary medulla; sc, subcortex. (From Motta 1969.)

the presence of a primary meristem in the rhizomorph apex. But he noted two types of meristematic activity: (1) the primary meristem that is located in the apical center, near the rhizomorph tip in which new hyphal elements are formed from apical initials; and (2) secondary meristems in the lateral regions of the apex where secondary cross wall formation takes place.

Differentiation of the apical initials involves synchronous nuclear divisions accompanied by segmentation in many planes. The apical initials are highly cytoplasmic, possessing non-membrane-bound fibrous bundles. Otherwise, they exhibit all the features normally found in hyphae of most basidiomycetes. The cells in the region assumed to be the primary meristem were shown by Motta to have dense cytoplasm with abundant ribosomes distributed throughout. Very few vacuoles were present and they were rather small. The number of nuclei per cell varied but could be quite high. The thickness of the initial wall remained constant during cell enlargement, indicating that the wall material was continuously synthesized in these cells. Schmid and Liese (1970) and Motta (1982) subsequently confirmed these findings.

Motta (1971) studied the histochemistry of the rhizomorph system. He found very high amounts of protein and nucleic acids, especially RNA, in the rhizomorph apical region. This discovery agrees with the view that this region is a true meristem. Large stores of glycogen were found in the cells adjacent to the meristem (i.e., apical center) and in the primary medulla (Motta 1971).

Wolkinger and others (1975) and Granlund and others (1984) studied rhizomorphs with the scanning electron microscope and discerned basically the same morphology described by Motta (1969) and Schmid and Liese (1970). Granlund and others (1984) used critical point drying which enabled them to better preserve the structure of the mycelia. This technique avoided hyphal collapse and allowed them to demonstrate that a loose network of hyphae (which they call the peripheral cover) covers the mature parts of the rhizomorphs. The method also enabled them to measure hyphal diameters in different regions of the rhizomorph and to calculate the resistance to solution flow through these hyphae (table 3.1). Obviously, from the values given in table 3.1 the hyphae of the medulla are the most likely candidates for solute flow-mediated transport in the rhizomorphs as was speculated by other previous au-

polyethylene bags to incubate rhizomorphs from logs of infected trees, they produced substantially larger rhizomorph apices with more clearly defined layers. The outer layers and the apical region were more densely packed with cells compared to those obtained by earlier studies. Their analyses of the morphology and formation of the mucilagenous layer confirmed the results of Hartig (1874), who described both long hyphae and swollen cells with a dense interior in the mucilage.

Mucilage was produced in tightly packed cells at the interface between the mucilagenous and cellular regions of the rhizomorphs. In this region, mucilage-containing vesicles coalesced with the plasma membrane, creating a mucilage-filled space between the membrane and all parts of the cell wall, with the septal plate being traversed by membrane-bound protoplasmic protruberances. After partial or complete digestion of the cell wall, this mass was released outside the cells.

Powell and Rayner (1984) found a specialized layer of cells, up to several cells wide, in the apical dome. These cells were biochemically very active as judged by their numerous mitochondria; and they were characterized by axial bundles of microfilaments, several of which occurred in each individual cell. These microfibril bundles were described earlier by Motta (1969). Powell and Rayner (1984) discussed the likelihood that this specialized layer of cells may provide a short-term supply of growth materials to the apical dome.

Some disagreement exists regarding the mechanism of rhizomorph growth which can be 19 mm or more per day. Brefeld (1877) and later Motta (1969) concluded that rhizomorph extension is due to a meristematic apical center containing actively dividing cells which give rise to the various other layers. This view was challenged by Rayner and others (1985), who suggested that rhizomorph extension might be analogous to the balanced lysis mechanism which has been proposed for

TABLE 3.1 — Diameter (μm), cross-sectional area (μm^2), and calculated resistance to solution flow (μm^{-2}) of hyphae of different rhizomorph layers.

Tissue	Diameter	Cross-sectional area	Resistance to solution flow
Cortex	2.3	4.15	0.24
Sub-cortex	4.7	17.35	0.085
Medulla	13.9	151.75	0.0065

Source: Granlund and others (1984)

thor Rayner (1983) studied the ultrastructural mucilage production by rhizomorphs. Using

hyphal extension (Bartnicki-Garcia 1973). In this model, extension is possibly mediated by a plasticized apical dome which is driven forward by pressure generated within a tube with rigid side walls (rind) and compensated for by branching and growth of the intercalated apical hyphae. Rayner and others (1985) considered that plasticization could be facilitated by mucilage production which disrupts the continuity of the hyphal mesh that covers the dome. Rigidity could be achieved by melanization and compaction of the outer (rind) crust, and forward pressure could be provided via osmotically driven flow through the medullary region. However, too little evidence is available to support conclusively the hypotheses of Rayner and others (1985). Also, the basically filamentous organization of the rhizomorph apices might be obscured in thin sections of the dense cells of the apical dome (Schmid and Liese 1970). For example, compare the scanning electron micrographs obtained by Granlund and others (1984) with Motta's (1969) transmission electron micrographs of thin sections. We must conclude that the mechanisms underlying growth and extension of rhizomorphs are far from being completely understood.

Organization of the Differentiated Rhizomorph

All authors agree on the basic structure of the differentiated rhizomorph: the outer layer consists of mucilage and a loose network of hyphae surrounding a melanized and densely packed cortex. The cortex is the main structure which protects the rhizomorph in soil from being colonized by fungi and bacteria. Presumably, the melanin content of the outer cell walls confers the protection (Bloomfield and Alexander 1967, Khuo and Alexander 1967). Below the cortex lies the subcortical layer which forms the transition to the medulla. A loose mesh of wide-diameter hyphae, the medulla, is the main structure responsible for the transport of water and nutrients (Jennings 1984). Towards the center of the rhizomorph, the medullary hyphae become more and more loose, forming finally a central canal which is the main structure of oxygen translocation (Smith and Griffin 1971).

At the substrate-air interface, growing rhizomorphs can form "breathing pores" (Smith and Griffin 1971) that allow oxygen to diffuse through the intertwining hyphae into the central canal. These structures resemble buds of rhizomorph branches but have a completely different morphology. They are formed by tufts of hyphae, perhaps of aborted side branches, that have burst through the rind of the rhizomorph. The apices of these branches are composed of loosely intertwined hyphae with no organized meristem and are directly connected with the central canal.

Uptake and Transport of Nutrients and Water

The earliest studies on the nature and physiology of mycelial cords proposed a definite role for them in the uptake and especially the transport of nutrients and water (e.g., Falck 1912). The importance of rhizomorphs for transporting oxygen to growing parts of the fungus was first elucidated by Munch (1909), whose data were confirmed by Reitsma (1932). Schütte (1956) demonstrated that when fluorescein was applied to the base of rhizomorphs, it was transported to the tips. Morrison (1975) studied the uptake of radioactively labeled chloride and phosphate plus the uptake of ammonium ions. The two labeled ions were readily taken up by rhizomorph tips. When applied to their bases, these ions were translocated to the tips, but not in the opposite direction. The immersion of rhizomorph tips into a medium containing ammonium stimulated production of amino acids. Anderson and Ullrich (1982b) basically confirmed Morrison's observation that the transport in actively growing rhizomorphs is acropetal. Using C-14 labeled glucose and P-32 labeled phosphate as isotopic markers, they showed that diffusion was not a mechanism of transport. Only rhizomorphs living under aerobic conditions were able to absorb and to transport the nutrients, suggesting that the mechanism of transport is dependent upon aerobic respiration. Rhizomorphs living under anaerobic conditions were able to absorb the radioactive label but not transport to it.

Eamus and Jennings (1984) determined the water, solute, and turgor potentials in *Armillaria* rhizomorphs and found a considerable gradient of water and turgor potential from the tip to the base of the rhizomorphs. From these data and cytological evidence, the three criteria that Zimmermann (1971) said must be fulfilled for pressure-driven flow to be accepted as a translocation mechanism in plants are fulfilled in *Armillaria* rhizomorphs. These criteria are: (1) the conducting channel must be relatively impermeable to water in a lateral direction; (2) it must be very permeable to solutes and water in a longitudinal direction; and (3) turgor gradients must exist between source and sink. Eamus and others (1985) measured the internal structure and hydraulic conductivity of rhizomorphs. Their data support the view that long-distance transport occurs predominantly by solutes moving along vessel hyphae of the medulla. Granlund and others (1985) measured the velocity of translocation, estimating it to be 0.55-10.8 cm.h⁻¹; the flux of carbon and phosphate was 0.07-3.8[nMcm⁻²s⁻¹]. They could not determine the chemical form in which carbon is translocated because of a rather vigorous lateral transfer, metabolism, and metabolic compartmentation of the label away from the stream within the rhizomorph. By changing the source-sink relations, they were able to demonstrate basipetal transport. In addition, bidirectional transport was observed.

The kinetics of phosphate uptake by rhizomorphs of *A. mellea* was studied by Cairney and others (1988). A biphasic mode of phosphate uptake indicated two different carrier systems with different Km and Vmax values. By chemically analyzing the homogenized rhizomorphs together with nuclear magnetic resonance studies of the intact system, they could discern between two orthophosphate pools, cytoplasmic and vacuolar, with most of the orthophosphate located in the vacuole. A significant portion of the cytoplasmic phosphorus was present in the rhizomorph as polyphosphate.

Concluding Comments on Rhizomorph Structure

Although development of *Armillaria* rhizomorphs has been studied for over 150 years, this process is still not well understood. Considerable work has been done on the structural and morphological features of rhizomorph development using both light and electron microscopes. But as will be evident later, virtually nothing is known about the biochemical mechanisms or genetic events that accompany their differentiation.

The morphology of rhizomorphs reveals a unique degree of differentiation. There are more than five types

of tissues with different ultrastructures and functions in the organ. This makes rhizomorphs the most highly differentiated vegetative tissues of fungi, reaching almost the degree of differentiation of a plant root. The order and function of the different specialized cells and cell regions are summarized in table 3.2.

The picture that emerges so far is that of a highly differentiated organ with some specialization regarding solute transport and gas diffusion. Because of these structural features, *Armillaria* can grow in a hostile environment and compete with the microbiota in the forest floor. In addition, this structure enhances the pathogenic potential, including the capacity to enter the intact surfaces of a tree (Woeste 1956). It may also confer some competitive advantage over other root disease fungi, such as *H. annosum* (Shaw 1989b).

Nutrition and Physiology

In *Armillaria*, as with other fungi, factors that control growth and development of morphological structures may do so through the activation of key physiological and biochemical processes. Therefore, their appropriate manipulation may lead to the elucidation of underlying processes and mechanisms that determine growth and development. Since factors affecting growth and development of rhizomorphs and associated physiological and biochemical changes have been the focus of many physiological investigations of *Armillaria*, these topics will be emphasized. But because of the paucity of data concerning some aspects of *Armillaria* physiology, relevant research involving other fungi is included.

Garrett (1953) was the first to systematically study the induction of *Armillaria* rhizomorphs in pure culture on defined media. Working with agar plates, he showed that the production of rhizomorph initials is controlled by nutritional factors. Below we discuss *Armillaria* nutrition and physiology, including factors that affect rhizomorph development. We emphasize two themes: "factors" and biochemical changes affecting growth and development.

Factors Affecting Growth and Development

Nutritional Factors

Carbon Sources

Armillaria can utilize a wide range of carbon sources. This can be inferred from the reports of its wide host range (Raabe 1962a, 1979b; Rishbeth 1983; Singh and Carew 1983) and studies that show that some isolates

TABLE 3.2 — Specialized cells and regions of the *Armillaria* rhizomorph and their proposed functions.

- | | |
|----|--|
| 1. | Gelatinous sheet and mucilage layer at the apex: |
| — | protects the apex and facilitates its growth in the soil |
| 2. | Central region of the apex: |
| — | associated with mucilage production |
| — | includes a central meristem responsible for the growth of the rhizomorph |
| 3. | Circum-medullary cells of the apex: |
| — | provide a short-range supply of growth material for the apical dome |
| 4. | Lateral meristem: |
| — | originates lateral growth behind the apex |
| 5. | Melanized cortex: |
| — | the outer rind of the rhizomorph which protects it against fungal and bacterial attack, owing to its melanin content |
| 6. | Subcortical layer: |
| — | the secondary meristem associated with lateral growth |
| 7. | Medulla: |
| — | large cells associated with solute-mediated transport of nutrients |
| 8. | Breathing pores: |
| — | regions in the rhizomorph which facilitate oxygen uptake by the organ |
| 9. | Central canal: |
| — | within the rhizomorph which enables it to translocate gases |

can utilize organic substrates for maintenance and growth in soil (Garrett 1960, Morrison 1982a) and on plant hosts (Rishbeth 1972b, Wargo 1980b). This view also is confirmed by the numerous reports that *Armillaria* can grow in culture on various carbon sources including carbohydrates (Wargo 1981a, Weinhold and Garraway 1966), lipids (Moody and Weinhold 1972a,b), phenols (Cheo 1982; Shaw 1985; Wargo 1983b, 1984), and alcohols (Weinhold 1963, Weinhold and Garraway 1966). The capacity of this fungus to fix CO₂ (Schinner and Concin 1981) suggests that this, too, may be a source of carbon for growth under certain conditions.

Despite the wide range of carbon sources they can utilize, *Armillaria* species seem to be selective in their ability to maximally utilize them for growth. For example, when glucose, fructose, and sucrose were compared, mycelia grew but were very sparse (table 3.3). This indicates that under these conditions these carbohydrates were used primarily as sources of energy for performance of vital functions and only sparingly for growth. In contrast, ethanol, added as a sole carbon source or as a supplement to a medium containing glucose, fructose, or sucrose, caused prolific growth of mycelia and rhizomorphs (table 3.3). Also, the fungus grew on ethanol-supplemented media containing glucose better than on fructose, which in turn was better than sucrose. Studies with C-14 labeled sugars suggest that these differences were partly related to different rates of uptake and utilization (Garraway 1975).

Examining the studies in which relative growth on various sugars was compared, one may conclude that *Armillaria* selectively utilizes carbon sources; glucose is the preferred carbohydrate. Moreover, when nutri-

TABLE 3.3 — A comparison of ethanol, glucose, fructose and sucrose, with or without an ethanol supplement, as carbon sources for mycelial growth and rhizomorph production by *Armillaria* in liquid culture.

Carbon Source (2.4 g/l)	Dry weight (mg.)			
	Ethanol (.24 g/l)	Mycelium	Rhizomorphs	Total
Ethanol	-	22	18	40
Glucose	-	0.8	0.0	0.8
Glucose	+	26	20	46
Fructose	-	2.6	0.0	2.6
Fructose	+	8	8	16
Sucrose	-	0.9	0.0	0.9
Sucrose	+	6	4	10

Source: Weinhold and Garraway (1966)

tional conditions change, the carbon source can shift from one which primarily maintains vital functions to one that both maintains these functions and supplies carbon for synthesis of compounds needed for growth and development.

As described later, such observations may help pathologists and ecologists interpret and explain certain in vivo aspects of *Armillaria* behavior. Presumably, when the interaction between *Armillaria* and a host is quiescent, there is limited access to host nutrients and growth promoters. Conversely, conditions associated with aggressive colonization of the host are likely to involve high access to host nutrients and growth promoters. Support for this view comes from studies such as those of Wargo (1972).

Nitrogen Sources

Besides a carbon source, *Armillaria* needs a suitable and adequate nitrogen source to grow and develop effectively. Garrett (1953) noted that *Armillaria* is not able to use nitrate as its sole nitrogen source. Also, although it grows on ammonium tartrate, the best growth was observed with amino acids. Similarly, Weinhold and Garraway (1966) studied how nitrogen sources affect growth and development of *Armillaria* in culture with glucose (0.5%) as a carbon source and ethanol (0.05%) as a growth stimulant. Casein hydrolyzate was the most effective nitrogen source followed by individual amino acids, several of which were more effective than inorganic nitrogen sources such as ammonium and nitrate (table 3.4).

TABLE 3.4 — A comparison of nitrogen sources for mycelial growth and rhizomorph production by *Armillaria* in liquid culture with ethanol (2.4g C/l) as carbon source.

Nitrogen Source (0.4 g N/l)	Dry weight (mg.)		
	Mycelium	Rhizomorphs	Total
Casein	12	102	114
L-Aspartic acid	25	80	105
DL-Glutamic acid	13	89	102
L-Alanine	23	75	98
L-Asparagine	20	75	95
L-Glutamine	21	61	85
Glycine	35	36	71
DL-Leucine	15	46	61
(NH ₄) ₂ HPO ₄	10	47	57
KNO ₃	3	0	3
Control—no nitrogen	7	0	7

Source: Weinhold and Garraway (1966)

The effectiveness of casein hydrolyzate is related to its composition of mixed amino acids, including glutamic acid and leucine, which support vigorous growth of the fungus. Also, its effectiveness may be related to amino acid uptake which, in fungi, is governed by amino acid specific transport systems (Pateman and Kinghorn 1976). Transinhibition or transport system shutdown occurs as system-specific amino acids accumulate inside hyphae (Horak and others 1977). The variety of amino acids supplied by a substrate such as casein hydrolyzate would permit more transport systems to operate, resulting in a greater total nitrogen uptake. The capacity of a fungus to utilize the available nitrogen source is largely determined by the amount and type of carbon source. For example, Garrett (1953) noted that the optimal concentration of nitrogen to induce rhizomorphs increased as the carbohydrate concentration in the medium increased.

Rykowski (1976a) studied the interrelations between carbon and nitrogen levels in culture media on mycelial growth and rhizomorph production in several isolates of *Armillaria*. He found that at an appropriate nitrogen level, more carbon increased the mycelial dry weight. However, at a given carbon level, an increase in nitrogen above a certain level inhibited growth. Thus, the C:N ratio which varies for different isolates was found to be decisive for rhizomorph development.

Inorganic Nutrients

The requirements of *Armillaria* for inorganic nutrients are assumed to be comparable to those reported for other fungi. On this basis, relatively large quantities of magnesium, phosphorus, potassium, sulfur, and to a lesser extent, calcium may be required whereas copper, iron, magnesium, zinc, and in some instances, molybdenum may be required in minute quantities. These nutrients may play the same physiological roles in *Armillaria* as in other fungi (Garraway and Evans 1984). Although no systematic study has addressed the effects of various concentrations of these essential inorganic nutrients on *Armillaria* growth and development, Morrison (1975) recognized that the availability of inorganic ions affected its behavior in soil.

Vitamins

The importance of certain vitamins for growth was studied systematically by Garrett (1953), who compared the responses to thiamine and biotin. He noted that thiamine was required for growth but biotin was not. Also, Garraway (1966) noted that one isolate of *Armillaria* grew optimally in a synthetic culture medium supplemented with ethanol when the only vitamin added was thiamine. When this medium was

deprived of thiamine, growth was reduced by 85%. In contrast, growth of this isolate was insensitive to either the presence or absence of biotin. Thus, except for thiamine, *Armillaria* appears to have the capacity, in common with many other decay fungi, to synthesize required vitamins from simple precursors (Garraway 1966).

Thiamine, as thiamine pyrophosphate, serves as the required coenzyme for several enzymes of intermediary metabolism that catalyze the removal or transfer of aldehyde groups. These include pyruvate carboxylase, transketolase, pyruvate dehydrogenase, and alpha-ketoglutarate dehydrogenase. Fungi are more often auxoheterotrophic for thiamine than for any other vitamin (Garraway and Evans 1984).

Organic Growth Factors

Several organic compounds produce rather dramatic effects on the growth and development of *Armillaria*. These compounds produce a response at concentrations substantially above those produced by typical vitamins, but far below those of nutrients such as carbon and nitrogen. Compounds which promote growth and development of *Armillaria* in this way include alcohols, auxin and related compounds, fatty acids, and phenols and related compounds.

Prior to 1963, optimal growth and development of *Armillaria* in defined media could be accomplished only by supplementation with undefined substrates such as yeast or figwood extract (Raabe 1962b, Weinhold and others 1962). In 1963, Weinhold discovered that low-molecular-weight alcohols and related compounds enhanced the fungus' growth and development (table 3.5). This made it possible to grow *Armillaria* on a completely defined medium and opened the way for critical studies on the nutrition and physiology of the fungus. Thus, in addition to being carbon sources, low-molecular-weight alcohols serve as organic growth factors in the sense described above. Growth was poor and rhizomorphs failed to develop on a synthetic medium containing glucose (0.5%) as the sole carbon source. But adding a small quantity (0.05%) of either ethanol, 1-propanol, or 1-butanol to the glucose medium stimulated prolific growth and rhizomorph formation (Weinhold 1963, Weinhold and Garraway 1966). Several other low-molecular-weight alcohols were shown to enhance growth and rhizomorph formation, but *Armillaria* isolates varied greatly in their ability to respond to different alcohols (Allermann and Sortkjaer 1973). These observations are of potential interest to those who study *Armillaria* ecology because soil microorganisms produce sufficient ethanol to promote rhizomorph development

TABLE 3.5 — Effect of ethanol-related compounds containing two carbon atoms, and other alcohols, in different concentrations, on rhizomorph production by *Armillaria*.

Conc. (mmole/ liter)	Length (cm) at 14 days*					
	Ethanol	Acetal- dehyde	Potassium acetate	Methanol	1-Propanol	1-Butanol
10.8	59.8+2.8	—	17.5+1.1	< 1.0	36.5+1.3	79.3+2.9
2.6	60.3+4.3	21.3+3.7	11.2+6.0	< 1.0	54.5+3.5	54.2+4.7
1.08	28.9+3.2	15.7+3.5	2.5+0.3		49.0+4.4	43.7+4.7
0.0	< 1.0	< 1.0	< 1.0	< 1.0	< 1.0	< 1.0

* Each value is the mean of at least six replications; standard error is indicated.

Source: Weinhold (1963)

(Pentland 1965, 1967); and ethanol may also be present in tree roots (Coutts and Armstrong 1976, Crawford and Baines 1977).

With the *Armillaria* isolate used by Weinhold, growth on a glucose medium supplemented with ethanol was equivalent to that on a medium containing ethanol (0.5%) as the sole carbon source (Weinhold and Garraway 1966). Analysis of the glucose culture medium at various times during the incubation period, however, showed that most of the growth occurred after the ethanol supplement was depleted from the medium (Garraway and Weinhold 1968b). This indicated that glucose was effectively used as a carbon source after a period of adapting to the ethanol supplement. When extra ethanol was added to a synthetic medium after 7 days (Garraway and Weinhold 1970) or 15 days (Sortkjaer and Allermann 1972) of incubation, the growth rate rose significantly. An increased growth-rate response to ethanol accompanied a decreased short-term uptake and utilization of glucose (Garraway and Weinhold 1968a, 1970) and an increased uptake of nitrogen and phosphate (Sortkjaer and Allermann 1973). Also, Sortkjaer and Allermann found that the rate of DNA and RNA accumulation increased as ethanol was added (fig. 3.7). These observations may provide clues to the mechanism(s) by which low-molecular-weight alcohols promote growth and development in *Armillaria*.

Several compounds with auxin activity promote growth and development of *Armillaria*. For example, synthetic media supplemented with 10 mg/l or more of indole-3-acetic acid significantly increased rhizomorph production (Garraway 1970, 1975). Also, 2,4-dichlorophenoxyacetic acid (2,4-D) stimulated the growth rate and amount of rhizomorphs produced by several isolates (Pronos and Patton 1979).

Such observations suggest that there is value in assessing models proposed to explain how auxins act on higher plants (Key 1969, Key and others 1967, Rayle 1973) to stimulate the growth of *Armillaria* rhizomorphs. The proposed response to auxin involving nucleic acid and protein synthesis might relate not only to the effects of auxin but to those of ethanol as well. According to this proposed mode of auxin action, the interaction of auxin with the plasma membrane releases a factor that moves through the cytoplasm and into the nucleus. The factor controls the activity of RNA polymerase in the nuclei and stimulates the synthesis of mRNA. The new mRNA is translated in the cytoplasm, resulting in new proteins which enhance cellular growth (Key 1969).

Lipids and fatty acids (Moody and Weinhold 1972a,b) and ortho- and para-aminobenzoic acid (Garraway 1970) strongly stimulate rhizomorph development when added to a defined basal medium. Since ethanol is linked metabolically to lipids and fatty acids (Garraway and Weinhold 1968a) and ortho- and para-aminobenzoic acids are linked metabolically to auxin, the possibility exists that all of these organic growth factors promote rhizomorph development by a common mechanism. Further molecular research will help to establish whether or not a common mechanism is involved in the response of *Armillaria* to these various growth factors.

Plant Extracts and Phenolic Substances

Many studies on *Armillaria* have reported that undefined media such as yeast extract or potato-dextrose-agar stimulate rhizomorph formation. Raabe (1962b) reported on the suitability of wood-based culture media for their stimulatory effect on rhizomorph induction. Also, Weinhold and others (1962) observed that a

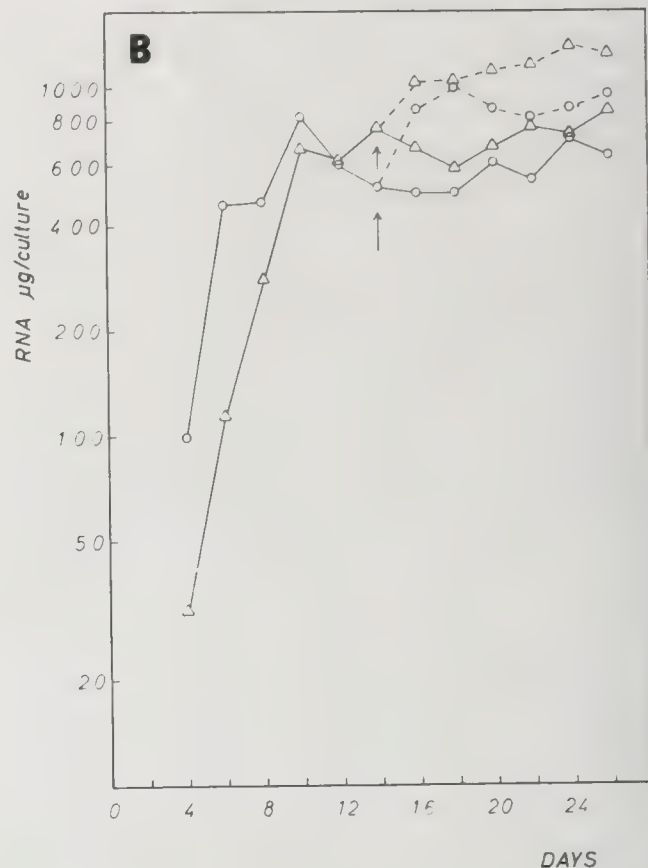
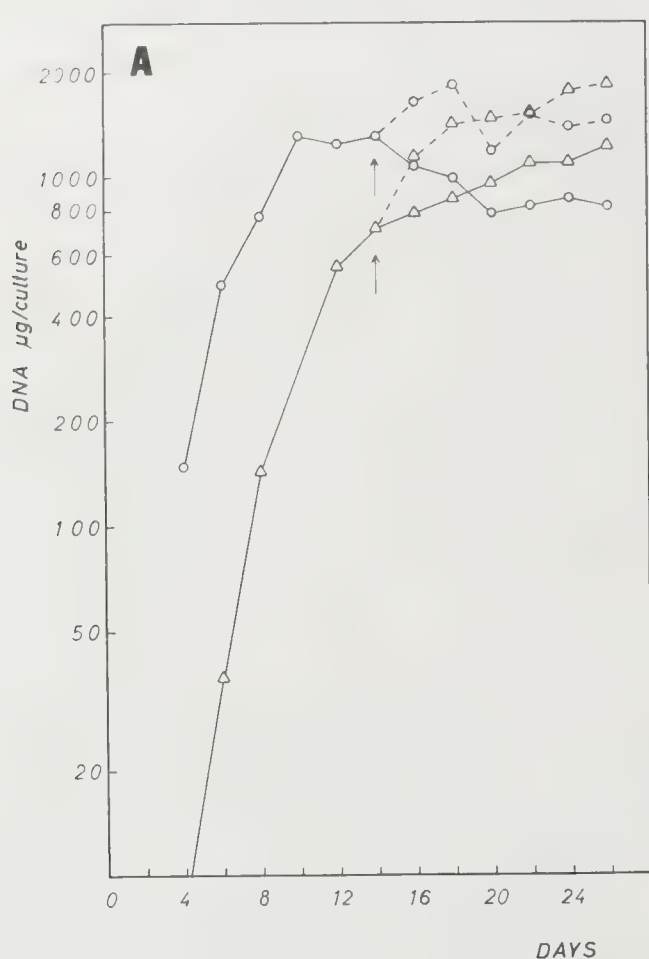


FIGURE 3.7 — DNA content (A) and RNA content (B) in *Armillaria* as a function of time following the addition of a boost of ethanol to culture media. The dashed lines show the content of DNA or RNA after the addition of extra ethanol;

arrows indicate the time of addition of the extra ethanol. O = Diphenylamine method for DNA, orcinol method for RNA; Δ = UV method for DNA or RNA (from Sortkjaer and Allermann, 1973).

partially purified extract of figwood stimulates rhizomorph initiation and growth even though chemical analyses suggested that some factors other than ethanol or related compounds might be involved. More recently, Lin and others (1985) studied the induction of rhizomorphs by substances present in bark. Their observations that various plant constituents are able to induce rhizomorphs have been confirmed by more recent studies with auxins and phenolic compounds.

During the last decade, *Armillaria* has been reported to variously respond to phenolic compounds. Perhaps these studies received some impetus from earlier work which concluded that ethanol may enhance rhizomorph development by inhibiting glucose uptake and its conversion to phenolic inhibitors (Garraway and Weinhold 1970). The "phenol inhibitor theory" received added support when Vance and Garraway (1973) found that ethanol altered the phenol composition and lowered phenol concentrations in the fungus. Moreover, they noted that extracts of *Armillaria* thalli grown on glucose media had high levels of phenol and inhibited growth whereas ex-

tracts of thalli grown on ethanol-supplemented media had lower phenol levels and were non-inhibitory. This theory received further support when Oduro and others (1976) partially characterized from *Armillaria* a phenolic compound with antibiotic properties.

Elevated levels of certain phenols may stimulate growth and rhizomorph production whereas other phenols may be inhibitory. Thus, mycelial growth was enhanced by as little as 10 mg/l of shikimic acid (a precursor of phenol synthesis), protocatechualdehyde, and p-hydroxy benzoic acid (Garraway 1970). Also, guaiacol (Edwards 1981, Edwards and Garraway 1981), tannic acid (Cheo 1982, Shaw 1985) and substances rich in lignin (Guillaumin and Leprince 1979) promoted growth and rhizomorph development. But gallic acid, a derivative of oak bark tannin, inhibited certain isolates of *Armillaria* (Cheo 1982, Shaw 1985, Wargo 1980a). Although Armillatox, a proprietary phenolic fungicide, has been shown to inhibit rhizomorph development from wood blocks (Rahman 1978), it was ineffective as a control agent (see chapter 11).

In recent years, attempts have been made to use growth on phenol-amended culture media as an aid in distinguishing species and genotypes of *Armillaria*. Wargo (1980a) reported the reactions of several isolates grown on a gallic acid medium both with and without ethanol. He suggested that growth differences on gallic acid-amended media may indicate differences in pathogenicity or virulence of isolates. However, this method of testing pathogenicity was found to be unreliable (Shaw 1985). Efforts to distinguish *Armillaria* species according to their growth habits on culture media amended with phenolic compounds have been reported (Rishbeth 1982, 1986). Shaw (1985) found differences in the growth habits of 21 isolates of several *Armillaria* species depending on whether the phenol amendment used was gallic acid (the hydrolyzed form of tannic acid) or tannic acid. This could reflect differences in the permeability of fungal cell membranes to these phenols. Such differences could confound efforts to use phenol-amended medium as an aid to distinguish among species.

Environmental Factors

Growth and development of *Armillaria* involves a complex interplay of metabolic processes and other intracellular events. Therefore, environmental factors should help shape the expression of metabolic events leading to morphological changes. In the previous section, effects of nutritional factors on growth and development were emphasized. Below, we discuss effects of environmental factors such as temperature, aeration, pH, light, soil organic matter, and soil organisms.

Temperature

The earlier studies of Benton and Ehrlich (1941) and Bliss (1946) may have prompted the more recent systematic studies of the effects of temperature on mycelial and rhizomorph growth (Rishbeth 1968). Such studies provide information useful in predicting the fungal behavior on natural substrates and in soil. In this regard, Rishbeth (1968) noted the optimum growth rates of *Armillaria* mycelia and rhizomorphs on malt agar were 0.75 mm/day and 9.8 mm/day, respectively, at 28°C. The optimum growing temperature varied with the conditions but was about 22°C for rhizomorph growth from woody inocula through tubes of soil and for mycelial sheets growing along woody stems. Rhizomorphs produced by *Armillaria* isolates from different parts of the world grew maximally at 20°C and minimally at either 10°C or above 26°C (Rishbeth 1978a). How temperature affects field behavior of *Armillaria* is discussed in chapter 4.

Aeration

The vigor of *Armillaria* growth in soil and on natural substrates is related to aeration and, to a lesser extent, CO₂ levels. For example, the dry weight of rhizomorphs was reduced when the concentration of O₂ was lowered or that of CO₂ raised (Rishbeth 1978a). These studies and those of Ono (1970), Singh (1981b), and Morrison (1976) suggest that aeration strongly affects the distribution of rhizomorphs in soils (see chapter 4).

Smith and Griffin (1971) reported that oxygen affects both the rate of growth and the form of rhizomorphs. They acknowledged that maximum growth depends on high rates of oxygen diffusion within the rhizomorph's central canals. However, a partial pressure of oxygen of 0.04 atm on their outside surfaces inhibits rhizomorphs. They believed this occurred because high partial pressures of O₂ stimulated the fungus to produce p-diphenol oxidase, and that catalyzed the formation of a brown pigment in the rhizomorphs. This pigment overlays the walls of the cells and probably prevents growth by blocking the uptake of nutrients or the disposal of waste products by the cells.

pH

Benton and Ehrlich (1941) investigated how pH affects various *Armillaria* isolates in culture. The optimum pH for growth on malt agar was 4.5 at 21°C and 5 at 25°C. Studies with other fungi suggest that pH influences a fungus' ability to absorb various nutrients (Garraway and Evans 1984). Accordingly, the pathogenicity and aggressiveness that *Armillaria* exhibits on soils with low pH (Redfern 1978, Singh 1983) may be related to the pH effect on nutrient uptake by the fungus.

Light

Light inhibits vegetative growth of *Armillaria* (Weinhold and Hendrix 1963). Doty and Cheo (1974) found that mycelial and rhizomorph growth were inhibited by up to 80% when cultured in continuous light. Growth was reduced about 60% when cultures of the fungus were illuminated for 12 hr/day. Even exposure of only 2 hr/day inhibited growth by about 50%. The inhibitory effect of light occurred with several isolates. It was most inhibitory to isolates producing abundant rhizomorphs and less inhibitory to less productive isolates. Evidently, not all isolates or species of *Armillaria* are inhibited by light. For example, Benjamin (1983) showed that *A. limonea* produced rhizomorphs in the dark whereas *A. novae-zelandiae* would not produce rhizomorphs without light. This difference has been used as a diagnostic feature to separate isolates of the two species (Benjamin 1983, Hood and Sandberg 1987).

Growth of other rhizomorphic fungi appears to be inhibited by light. For example, Makambila (1978) noted that exposing cultures of *Rosellinia quercina* Hartig to light for 20 hr/day may inhibit rhizomorph growth up to 50%.

Soil Organic Matter

In vitro nutritional studies of *Armillaria* help validate the interpretation of field studies undertaken to evaluate the nutritional role of soil organic matter. Morrison (1976, 1982a) indicated that rhizomorphs absorb and utilize nutrients from soil and that soils rich in organic matter supply more nutrients for rhizomorph growth.

Effect of Other Organisms

Pentland (1965) observed that rhizomorph development was stimulated in pure culture by *Aureobasidium pullulans* (de Bary) Arnaud and attributed this effect to ethanol produced by this fungus (Pentland 1967). Also, Watanabe (1986) tested 121 fungal isolates for their ability to stimulate rhizomorph production either by co-culturing them with *Armillaria* or by amending *Armillaria* culture media with culture broth of the tester strain. He observed that 37 of the isolates tested effectively induced rhizomorphs. The most effective genera were *Macrophomina*, *Gliocephalis*, *Diploidia*, and *Sordaria* together with two unidentified species of Deuteromycotina. His reports did not include information on the chemical nature of the stimulatory factors involved.

Genetic Factors

Most researchers now acknowledge that species of *Armillaria* that occur worldwide comprise a complex of populations with distinctive genetic compositions (see chapters 1 and 2). Since genetic factors determine the expression of physiological and biochemical processes, genetic variation in *Armillaria* could be involved with reported cultural (Raabe 1966b) and pathogenic variations (Raabe 1967). Similarly, variation observed among *Armillaria* isolates in their responses to nutritional and environmental stimuli could be at least partially related to genetic differences. Examples cited previously include growth variation in response to low-molecular-weight alcohols (Allermann and Sortkjaer 1973), gallic acid (Cheo 1982, Shaw 1985, Wargo 1980a), and light (Benjamin 1983, Doty and Cheo 1974). However, nothing is known of the precise relationship between genetic control of responses to nutritional and environmental stimuli and the biochemical events involved. Also, the possible contribution of virus-like particles (Reaves and others 1988) to variation among *Armillaria* isolates should be consid-

ered. Chapter 6 provides further discussion of genetics in relation to pathogenicity and virulence.

Biochemical Changes Associated with Growth and Development

Voluminous literature relates biochemical changes to growth and development in fungi (Burnett and Trinci 1979, Moore and others 1985, Smith and Berry 1978); but the precise ways in which these changes regulate these phenomena are not known. However, studies of how biochemical changes relate to development in fungi provide clues to the regulatory mechanisms involved. A scan of the published literature suggests that many aspects of *Armillaria* biochemistry are either unknown or poorly understood. Therefore, formulating a good working hypothesis that implicates biochemical mechanisms in the pathogen's growth and development is difficult. We now focus on two biochemical themes that could have relevance to the regulation of growth and development of *Armillaria*: cell-wall polysaccharides and other macromolecules, and phenoloxidizing enzymes.

Cell-wall Polysaccharides and Other Macromolecules

Because cell walls control the shape of fungal cells and thalli, their composition and structure have been given particular emphasis in developmental studies. Ethanol, at concentrations that promoted growth and rhizomorph development, increased the incorporation of glucose into cell-wall polysaccharides by over 50% (Garraway and Weinhold 1968a, 1970). This could mean that cell-wall polysaccharide biosynthesis plays a part in the growth response (i.e., basidiome or rhizomorph formation) to various stimuli, as indicated in studies with other fungi (Stewart and Rogers 1978, Sietsma and Wessels 1977, Wang and others 1968, Wessels 1966). For example, the ratio of R-glucans (alkali-insoluble, highly branched beta-1,3- and beta-1,6 glucan) to S-glucans (alkali-soluble, alpha-1,3-glucan) was reported to change during basidiome development of *Schizophyllum commune* Fr. (Wessels 1965). Also, changes in cell-wall polysaccharide composition were correlated with genetically controlled changes in morphology in this fungus (Wang and others 1968). Moreover, cell-wall polysaccharide fractions from an *S. commune* mutant that failed to develop fully formed basidiomes were resistant to enzyme solubilization, whereas the same fractions from the wild-type isolate were soluble (Wessels 1966). Similar studies applied to *Armillaria* might help elucidate the role of cell-wall biosynthesis in its growth and development. A complex carbohydrate was recovered from mycelial cultures of *Armillaria* and some of its components have been char-

acterized (Bouveng and others 1967). But the importance for morphogenesis, if any, is not known.

Changes in large molecules not associated with the cell walls also occur during growth and development. For example, DNA and RNA contents of *Armillaria* increased at three times the rate of the dry weight in the first few days after ethanol was added to thalli (Sortkjaer and Allermann 1973). Also, similar increases in protein were observed in response to ethanol (Garraway unpublished). Thus, ethanol at concentrations which promote growth and development of *Armillaria* caused an early increase in constituents needed for nuclear division as well as for protein synthesis.

An association between lipids and growth and rhizomorph production in *Armillaria* was suggested from studies with C-14 labeled ethanol (Garraway and Weinhold 1968a). *Armillaria* preferentially incorporated ethanol into lipids. Furthermore, lipids of the type which are assumed to be present in *Armillaria* and its natural substrates, including lecithin, oleic acid, and linoleic acid, were able to replace ethanol as promoters of rhizomorph production (Moody and Weinhold 1972a,b).

Enzymes

Diverse enzyme studies have attempted to establish clues to the biochemical factors which regulate growth and development in fungi. Although changes in various enzymes have been reportedly correlated with morphogenesis, they are probably secondary to the more fundamental changes involved. This view is supported by studies involving enzyme levels and isoenzymes in *S. commune* (Bromberg and Schwalb 1978, Ullrich 1977). Work with *Armillaria* dehydrogenases are relevant in this regard. Mallett and Colotelo (1984) analyzed the activity and isoenzyme pattern of alcohol dehydrogenase during ethanol-induced rhizomorph formation. They found a significant increase both of the enzyme activity and the number of isoenzymes of alcohol dehydrogenases in the rhizomorphs but not in the mycelium. The relevance of the biochemical event studied appears obvious: alcohol dehydrogenase is needed for the metabolism of ethanol. But the relevance of this biochemical event to rhizomorph morphogenesis is still an open question.

Currently, some researchers are evaluating how the observed correlation between phenoloxidizing enzymes and rhizomorph development affects morphogenesis. The association of phenoloxidizing enzymes with rhizomorph growth received increased attention with the report that O₂ partial pressures above 0.04 atm at

the rhizomorph surface enhanced accumulation of a brown pigment and inhibited its growth (Smith and Griffin 1971). Since high O₂ partial pressures stimulated the activity of p-diphenol oxidase, they proposed that the pigment formed as a result of enzymatic polymerization of phenols. Electron micrographs revealed that the pigment became localized in the intracellular spaces of the rhizomorphs. Smith and Griffin (1971) proposed that the pigment inhibited rhizomorph growth because an impermeable layer of polymerized phenol formed and it probably prevented the uptake of nutrients or the disposal of waste products by the cells.

More recently, Worrall and others (1986) have proposed a stimulatory role for laccase in rhizomorph initiation and development. Evidence supporting their claim includes several correlations. Ethanol and other substances that induced rhizomorphs in *Armillaria* also induced laccase (phenol oxidase) formation. In a range of isolates, rhizomorph production and laccase activities were positively correlated. Laccase was first detected just before the appearance of rhizomorph initials. Laccase activity peaked when rhizomorph growth was highest and fell to near zero when rhizomorph growth ceased. Laccase was not detected in cultures which were not induced to form rhizomorphs. Also, laccase activity and rhizomorph production, but not mycelial growth, were decreased by enzyme inhibitors with activity against laccase.

The contrasting interpretations of the role of phenoloxidizing enzymes by Smith and Griffin (1971) on the one hand, and by Worrall and others (1986) on the other, could involve different species of *Armillaria*. But contrasts are commonly encountered in *Armillaria* research. Edwards (1981) and Garraway and Edwards (1983) found that on a synthetic medium with casein hydrolyzate as the nitrogen source, a supplement of guaiacol (200 mg/l) promoted rhizomorph formation and increased phenoloxidizing enzyme (presumably laccase) activity. In contrast, when casein hydrolyzate was replaced with L-asparagine as the nitrogen source the same guaiacol supplement increased phenoloxidizing enzyme activity but not rhizomorph development. Adding an ethanol supplement to a medium containing guaiacol increased the activity of a laccase-like phenoloxidizing enzyme as well as rhizomorph growth. Thus, phenoloxidizing enzyme activity in *Armillaria* is apparently correlated with, but is not causatively related to, rhizomorph production in response to ethanol and other substances. Marsh and Wargo (1989) observed a similar association of laccase activity and rhizomorph formation among isolates of five species of *Armillaria*. Among the isolates that produced rhizomorphs, there was an association of higher laccase activity with greater rhizomorph production. Some iso-

lates, however, had laccase activity but produced no rhizomorphs (Marsh and Wargo 1989).

Phenoloxidizing enzymes have been implicated in the regulation of morphogenesis and differentiation of sporulating and resting structures in basidiomycetes and other fungi including *S. commune* (Leonard 1971, 1972, Phillips and Leonard 1976, Wessels and others 1985), *Coprinus congregatus* (Bull. ex St. Amans) Fr. (Choi and others 1987, Ross 1982), *Lentinus edodes* (Leatham and Stahmann 1981), *Podospora anserina* (Ces.) Niessl (Esser 1968, Molitoris and Esser 1971), *Sclerotium rolfsii* Sacc. (Chet and others 1972, Miller and Liberta 1977), and *Sclerotinia sclerotiorum* (Lib.) deBary (Wong and Willetts 1974). Very likely, they are important in these processes in *Armillaria* as well.

Nature of Phenoloxidizing Enzymes Produced by *Armillaria*

Because of the proposed causative association between rhizomorph morphogenesis and phenoloxidizing enzymes, the nature of these enzymes and their production by *Armillaria* needs to be reviewed. We do so giving consideration to the terminology for describing phenoloxidizing enzymes and the substrates used in their assay (Mayer 1987, Mayer and Harel 1979).

The commission on enzymes refers to monophenol monooxygenase (tyrosinase) as 1.14.18.1, diphenol oxidase (catechol oxidase, diphenol oxygen oxidoreductase) as 1.10.3.2, and laccase as 1.10.3.1 (Mayer 1987). This new classification differentiates between two reactions of the same enzyme, 1.14.18.1 for the cresolase activity and 1.10.3.2 for the catecholase activity of the same enzyme, catechol oxidase (Mayer 1987). Mayer proposes the general terms of "catechol oxidase" and "laccase" as the least confusing terms to use. Catechol oxidase can oxidize monophenols (tyrosinase or cresolase activity) or o-diphenols (catecholase activity); it cannot oxidize p-diphenols and this is diagnostic (Mayer and Harel 1979). Laccase can oxidize a wide range of substrates including mono-, di-, and tri-phenols. It can oxidize both o- and p-diphenols and its ability to oxidize p-diphenols is diagnostic (Mayer and Harel 1979). Catechol oxidase (tyrosinase) in fungi is primarily an intracellular enzyme and may have a role in melanin formation. Laccase is commonly excreted by fungi and has roles in lignin oxidation and degradation and detoxification of antifungal phenols in plant tissues (Mayer and Harel 1979).

Peroxidase (1.11.1.7) also catalyzes the oxidation of phenols by hydrogen peroxide (H_2O_2) and is non-specific for phenols. Much of the polyphenol oxidase activity reported in the *Armillaria* literature could be laccase activity if H_2O_2 commonly present

in cell-free preparations was not removed. For example, Mallett and Colotelo (1984), using 4-aminoantipyrine, a substrate specific for peroxidase, detected peroxidase in exudates from *Armillaria* rhizomorphs. Also, they used catechol to detect phenol oxidase activity in the exudates. Since catechol is oxidized by tyrosinase, laccase, and peroxidase, a proportion of the phenol oxidase activity detected included peroxidase. These workers also noted the presence of beta-glucosidase, acid protease, and alkaline protease in the exudates.

Peroxidase activities were also reported in rhizomorph extracts of *Armillaria* by Lanphere (1934) and Lyr (1955). However, no substrate specific for peroxidase activity was used nor was catalase added to extracts to destroy H_2O_2 and eliminate peroxidase activity.

Both tyrosinase and laccase activities have been reported in mycelial extracts of *Armillaria* (Käärik 1965); but laccase can oxidize both tyrosine and guaiacol (p- and o-diphenols), the two substrates used. Both tyrosinase (catechol oxidase) and laccase activities were based on visual color development in tubes with agar and either guaiacol or tyrosine as substrates in the growth medium.

Stronger evidence for laccase (p-diphenol) activity was reported in rhizomorphs of *A. mellea* (Jacques-Felix 1968) and *A. elegans* (Smith and Griffin 1971), the latter now known to be *A. luteobubalina*. Worrall and others (1986), working with several *Armillaria* species, detected true laccase activity in culture liquid using 2,6-dimethoxyphenol and p-phenylenediamine as substrates. They found a general relationship of laccase production and species of *Armillaria* related to the proclivity of each species to produce rhizomorphs. *Armillaria mellea* isolates tended to have relatively high laccase activity and rhizomorph production, *A. ostoyae* isolates had low laccase activity and low rhizomorph production, and *A. gallica* had a broad range of laccase activities and rhizomorph production. No peroxidase activity was detected in these studies; however, only one of the isolates was screened for peroxidase activity (Worrall and others 1986).

Recently, Marsh and Wargo (1989) assayed phenol oxidases over time in three isolates from each of five biological species of *Armillaria*: NABS I (*A. ostoyae*), NABS III (*A. calvescens*), NABS V (*A. sinapina*), NABS VI (*A. mellea*), and NABS VII (*A. gallica*). Laccase (tetramethyl-benzidine=TMB=substrate) and peroxidase (TMB with and without catalase=substrates) were detected in extracts from mycelium and rhizomorphs and in the extra-cellular growth medium. Peroxidase activity was confirmed by the lowering of oxidase activity when H_2O_2 in the extract was destroyed by adding

catalase, and by assay with a substrate specific to peroxidase activity, aminoantipyrine. Peroxidase activity was not detected in all isolates, and a broad range of activities among the isolates with detectable peroxidase activity did occur. Tyrosinase activity (dihydroxyphenylalanine=L-DOPA= substrate) was found only intracellularly. They detected a general relationship of higher laccase activity with greater rhizomorph production among rhizomorph-producing isolates. However, laccase activity was also present in some isolates that produced no rhizomorphs.

Conclusions

The foregoing discussion of nutritional and environmental factors affecting *Armillaria* indicates that principles of fungal nutrition and physiology may be applicable to some aspects of its behavior in soil and on infected hosts. On the other hand, the discussion of biochemical factors that regulate growth and development indicates major information gaps for fungi in general and *Armillaria* in particular. More basic information at the molecular and biochemical levels is needed to develop a good working hypothesis to explain regulation of growth and morphogenesis in response to nutritional and environmental factors. When this information becomes available, more effective approaches to manipulating *Armillaria* in culture, in soil, and on its many hosts may be forthcoming.

Miscellaneous Themes in the Physiology of *Armillaria*

Protease

A protease with unique properties has been recovered from *Armillaria* (Broadbent and others 1972). This enzyme cleaves peptide bonds which are N-terminal to lysine residues in proteins (Hunneyball and Stanworth 1975, Lewis and others 1978). This specificity for lysine residues in the protein is maintained even when the positive side chain of the lysine is formylated and thus neutral in charge (Barry and others 1981).

The enzyme is very stable in the presence of denaturing detergents such as sodium dodecylsulfate. Because of this feature, the enzyme can be used to fragment proteins which are insoluble in water but can be solubilized by the addition of detergent (Barry and Doonan 1987). No information is available on the biological role of the enzyme. Whether it is secreted into the environment or present at unique points in the developmental cycle, such as during basidiome formation, is not known.

Antibiotics and Other Metabolites

In 1951, *Armillaria* was observed to exhibit considerable antibiotic properties when cultivated either on wood, solid media, or liquid media (Oppermann 1952). *Armillaria* antibiotics inhibited other fungi as well as bacteria. These findings were confirmed by Richard (1971). Later, Ohr and Munnecke (1974) found that the production of these antibiotics was considerably reduced when *Armillaria* was fumigated with sublethal concentrations of methyl bromide. The authors suggested that this is one reason for the effect of soil fumigation. It may predispose *Armillaria* to attack by biological control agents such as *Trichoderma* that would otherwise be restricted by the fungus' own antibiotics (see chapter 11).

The chemical nature of the antibiotic substances and other metabolites produced by *Armillaria* was elucidated in subsequent years by several groups of scientists. Oduro and others (1976) isolated four chloroform-soluble substances for which antibiotic activities were determined by bioassays with either *Bacillus* sp. isolated from fumigated citrus roots naturally infected by *Armillaria* or cultures of *Cladosporium cucumerinum* Ellis and Arth. The authors were able to show that antibiotic activity was produced by all 17 *Armillaria* isolates used.

Detailed studies by several authors (Ayer and MacCauley 1987, Donnelly and others 1982, Jungshan and others 1984, Midland and others 1982, Obuchi and others 1990) have revealed that various isolates of *Armillaria* have at least 10 different compounds with antibiotic properties. Two aspects of the chemical nature of these substances are rather interesting. First, they are mostly complicated sesquiterpenoid esters, some belonging to the protolludane group. The organic acid to which they are bound is, suprisingly, the same substance which has been identified as the antibiotic substance of *Sparassis crispa* Wulf.: Fr. (Falck 1907, 1909, 1924, 1930). Second, these compounds contain a rather simple aromatic, Sparassol or orsellinic acid, which in all tests exhibits high antifungal and antibacterial activity (Cwielong 1986). Apparently, *Armillaria* uses the same chemical weapon as does *S. crispa* with the modification that sesquiterpenoids are attached to the aromatic group. Thus, the *Armillaria* antibiotics would penetrate more easily through membranes and would probably be more toxic than the unsubstituted Sparassol.

The variety of antibiotic substances produced by *Armillaria* and their high toxicity against microbes may explain, in part, why this fungus is so successful in its natural habitat and also some of its medicinal properties. For example, folklore of early American loggers

tells of woodsmen who would wrap their wounds from accidental cuts in an *Armillaria* fan. This protected them from further irritation and enhanced healing. Also, tablets containing artificially cultured mycelia of *Armillaria* are used in China for treating of dizziness, headache, neurasthenia, insomnia, numbness in limbs, and infantile convulsions (Jungshan and others 1984).

Bioluminescence

Bioluminescent fungi have interested biologists for some time (Glawe and Solberg 1989). More recently, attention has been given to the biochemical mechanisms involved (Airth and others 1966, Danilov 1987).

Armillaria is one of several bioluminescent basidiomycetes (Guyot 1927). Airth and Foerster (1960) prepared a self-portrait of a 15-day culture of *Armillaria* that showed high luminescence in the peripheral region (young cells) and less in the central area (older cells). A similar, more precise study using photomicrography and a different species of *Armillaria* (Berliner and Hovnanian 1963) showed light emission occurred throughout the entire cell.

The characteristics of the light emitted by *Armillaria* and other fungi have been investigated. Airth and Foerster (1960) noted the emission maximum of 528 nm was similar to that of other fungi but different from that of bacteria. They found that the energy of activation for emission in *Armillaria* is 17,500 calories with a temperature optimum of 26°C. Berliner (1961) suggested that fungi which exhibit bioluminescence may emit some waste energy of oxidation as light instead of heat. Also, Berliner noted that *Armillaria* took a longer time than other fungi studied to attain maximum light emission values, but sustained luminescence of 10 weeks equaled or exceeded that of other fungi.

Effect of Environment, Nutrition, and Growth Factors

The effects of temperature, exposure to X rays and ultraviolet light, nutrition, and growth factors on luminescence in *Armillaria* and other fungi have been reported.

Temperature

Light emission was low at -10°C and low or non-existent above 40°C (Airth and Foerster 1960) with the optimum temperature in the range of 18-26°C. Berliner (1961) found a similar optimum temperature for light emission in several basidiomycete fungi including

Ultraviolet and X-irradiation

Ultraviolet irradiation inhibited light emission from *Armillaria* and other fungi (Airth and Foerster 1960, Berliner 1963, Berliner and Brand 1962). The effects observed varied with the wavelength of incident radiation, the time elapsed, and the fungal species used. In contrast, X-irradiation enhanced luminescence from *Panellus (Panus) stipticus* (Bull: Fr.) P. Karst. (Berliner 1961) and probably would produce a similar effect on *Armillaria*.

Nutrition

The relationship between light emission and nutrition has been reviewed (Harvey 1952). Airth and Foerster (1965) reported a specific pH and nitrogen source for optimum light emission by *Collybia velutipes* (Fr.) Sing. On this basis, optimal nutritional conditions for maximum light emission presumably exist for *Armillaria* as well.

Growth Factors

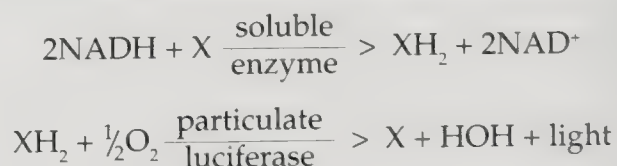
Luminescence in *Armillaria* responds to growth factors according to the concentration and type of factor used. For example, the light output was intensified more than 150% when *Armillaria* was grown on a medium containing 0.75 mg/l of biotin. Also, kinetin at 0.25 mg/l increased light output, but 6-benzylaminepurine had no effect (Berliner and LaRochelle 1964). The effects of antibiotics on light emission have also been studied (Berliner 1965).

Mechanism of Fungal Bioluminescence

Studies with *Armillaria* and other fungi have identified the key biochemical steps involved in fungal bioluminescence. For example, Airth and Foerster (1962) presented evidence that fungal bioluminescence involves the following:

- either reduced nicotinamide adenine dinucleotide (NADH) or reduced nicotinamide adenine dinucleotide phosphate (NADPH);
- an electron acceptor found in hot water extracts;
- soluble dehydrogenases;
- molecular oxygen;
- the particulate enzyme luciferase.

The proposed reaction involved in light emission is:



The similarities and differences of light emission between fungi and bacteria have been noted (Airth and others 1966). However, fungal and bacterial bioluminescence and chemoluminescence may have close links not only in their physical nature but in their biochemical nature as well.

Physiology of Host-Pathogen Interactions

Understanding the physiological bases for pathogenesis and the interactions of *Armillaria* species with their hosts is the key to understanding the variation in pathogenicities among and within the species of *Armillaria* that we now know. Unfortunately, much of the work that has been conducted in this area lacks essential taxonomy of the fungus. Results of these studies, therefore, may reflect the physiology of a single species, one or several genotypes within a species, or several different species all interacting with hosts that may or may not be resistant. Our current understanding, and hence what is presented herein, of what stimulates and controls penetration and colonization of a substrate by *Armillaria* is incomplete for any single species. What we know is probably a composite of several different *Armillaria* species interacting on susceptible and resistant hosts.

Genetic Control

The infection processes, resistant reactions, pathogenicity and virulence, and disease development within the host tree are discussed in chapters 4, 5, and 6. These processes represent host-pathogen interactions and involve the physiology of metabolic regulation of the fungus and host. Metabolic control of these interactions is determined by the genetic control of the physiological processes as modified by the environment (Daly 1976).

The reaction of host and fungus, therefore, depends on the host species that is attacked, the species and perhaps genotype of *Armillaria* that is attacking, and the environmental conditions under which host and fungus are growing. Most historical information on host-pathogen interactions focuses on the differences in response among host species. Little attention has been paid previously to differences in the pathogen since it was considered for the most part to be a single species. Now that several species of *Armillaria* are recognized with different pathogenic capabilities on different hosts (Davidson and Rishbeth 1988; Rishbeth 1982, 1985b), previous reports on host-pathogen interactions must be re-examined.

The infection process is both mechanical and enzymatic. Since penetration of the outer bark is reportedly similar in both the susceptible and the resistant reactions, subsequent colonization of the inner bark and cambial zone tissues differentiates the susceptible from the resistant reaction (Thomas 1934). These observations are based on reactions of hosts with single isolates of unknown species of *Armillaria*, although some attempts have been made to assign species names to some isolates used in these historical studies (see chapters 4 and 6). Whether all species of *Armillaria* can successfully penetrate the outer bark is not known. Wounding of the roots can enhance infection by *Armillaria* (see chapters 4 and 7), and perhaps some species of *Armillaria* are unable to penetrate intact bark.

Metabolic Control

Little work on the metabolism of *Armillaria* species in association with their hosts has been conducted. Therefore, mostly metabolic capabilities of *Armillaria* and their potential for interacting with hosts are reported here.

Pathogen Factors

Suberinase

Bark apparently offers limited resistance to penetration by *Armillaria*. Even periderms formed in response to the penetrating hyphae are unable to contain its growth (Rykowski 1975, Thomas 1934). The fungus can apparently grow faster than developing periderms and invades around them (Rykowski 1975) or penetrates directly through the periderms, probably by enzymatic activity (Arthaud and others 1980, Rykowski 1975, Thomas 1934). *Armillaria* can degrade suberin. Swift (1965) reported that the fungus, grown on ground bark of *Brachystegia spicaeformis*, caused a 59% loss in suberin content of the bark. *Armillaria* also produced hydrolytic enzymes when grown for 10 months on 0.5% raspberry suberin medium supplemented with salts, thiamine, and ethanol (Zimmermann and Seemüller 1984). Concentrated enzyme preparations from culture fluids caused up to 1% dry weight loss of suberin preparations after 16 hr incubation. Gas chromatographic analyses of the released material indicated that the components constituted a major part of the aliphatic monomers present in suberin (Kolattukudy and others 1981). How important suberin degradation is in the infection process is uncertain.

Polyphenol Oxidases

Armillaria produces phenol oxidases during the infection process. Discoloration, especially browning of

tissues, has been observed commonly during the infection and colonization process (Rykowski 1975; Thomas 1934; Wargo 1977, 1984a). Discolored bark in advance of colonized bark in black and white oaks had significantly less total phenols and more oxidized phenols than contiguous or noncontiguous healthy bark (Wargo 1984a). In colonized bark, total phenols were only 22% and 46%, respectively, of that in healthy bark of black and white oaks; and oxidized phenol levels were 3 and 3.5 times greater than in healthy bark (table 3.6). Phenol levels in discolored bark from wounded only bark tissues were also lower after 4 weeks than in healthy contiguous bark, but not as low as in colonized bark. Levels of oxidized phenols in discolored bark from wounded-only tissues did not increase as much as in colonized tissues.

Oxidation of the phenols in root tissues can result from both fungal and host polyphenol oxidases. No reports distinguish between host and fungus-mediated phenol oxidation. Fungal enzymes can oxidize phenols as a result of separate or combined effects of peroxidase, tyrosinase, or laccase depending on the phenolic substrates. *Armillaria* possesses all three enzyme activities and peroxidase and laccase can be secreted to oxidize phenols extracellularly, as described previously in this chapter.

Very limited information details the role of phenoloxidizing enzymes in the pathogenic process. Marsh and Wargo (1989) screened three isolates each of *A. ostoyae*, *A. calvescens*, *A. sinapina*, *A. mellea*, and *A. gallica* for production of constitutive phenol oxidases. Many, but not all, of these isolates were rated by other researchers in pathogenicity studies. The pathogenicities of the remaining isolates were rated by Marsh and Wargo as high, moderate, or low, based on their association with the host tree from which they were isolated. No obvious correlations of constitutive enzyme levels with pathogenicity were detected.

Phenols and other host substances can inhibit hydrolytic enzymes of fungi, thus restricting their activities on host cell walls and membranes and preventing infection and colonization. Polyphenol oxidases cause the oxidation and polymerization of compounds that are potentially toxic to the fungus, allowing infection and colonization to proceed in tissues rich in phenols. This reaction is apparent at the leading edge of mycelial fans colonizing living tissue. Here, an advancing band of oxidized (browned) tissue precedes the advancing mycelium (fig. 3.8). There is some evidence that these brown pigments induce wilt in infected plants. Thornberry and Ray (1953) isolated a dark brown protein-like pigment produced by *Armillaria* in liquid me-

TABLE 3.6 — Changes in mean concentrations of soluble phenols and their oxidation products effected by *Armillaria* in bark of roots of black and white oak trees naturally colonized by the fungus.

Species and tissue state	Phenols ¹ total	Tannins ¹			Phenols ² oxidized
		Total	Hydrolyzable	Condensed	
		mg phenols/g tissue			
Black Oak					
Healthy, control	167a	128a	143a	13a	238a
Healthy, contiguous	161ab	124ab	136a	13a	243a
Discolored	145b	107b	61b	11a	306a
Colonized	37c	31c	22c	8b	731b
SE	±5	±5	±3	±2	±30
White Oak					
Healthy, control	196a	147a	147a	15a	352a
Healthy, contiguous	170a	136a	160a	8b	621ab
Discolored	158a	124a	107b	9b	742b
Colonized	90b	67b	63c	11ab	1235c
SE	±10	±10	±8	±2	±80

Vargo (1984a)

al and hydrolyzable tannins - mg tannic acid equivalents/g freeze-dried bark: condensed tannin - mg catechin equivalents/g. Significant differences by ANOVA and Tukeys studentized range test (P≤0.05) indicated by different letter.

100 mg bark in 10 ml water at 450 nm and 1 cm light path used as estimate of oxidized phenols.



FIGURE 3.8 — Discolored brown zone in both bark and wood in advance of the mycelium. Note rhizomorphs on surface of primary root. (P. Wargo)



FIGURE 3.9 — Advanced decay of root wood by *Armillaria* (also note discolored brown zone in advance of mycelium). (P. Wargo)

dium. The pigment induced wilt in tomato seedlings and peach twigs at low concentrations. There is, however, no evidence that this mechanism operates in large mature trees.

These phenoxidizing enzymes are also important in wood degradation (fig. 3.9). *Armillaria* is classified as a white-rot fungus because it degrades and removes the lignified material from the cells, leaving the white cellulose and hemicelluloses somewhat intact (Campbell 1931, 1932). Campbell also found that decay of wood by *Armillaria* was somewhat atypical of most white-rot fungi in that lignin degradation in laboratory tests was limited compared to cellulose degradation. Scurti (1956), however, grew *Armillaria* in vitro on pure cellulose and pure lignin, and observed that lignin was degraded but not cellulose. Whether these results reflect differences among species of *Armillaria* cannot be answered.

The ability to decay wood is probably quite different among species of *Armillaria*, and studies with known species are necessary. Marsh and Wargo (1989) found that some species of *Armillaria* produced high constitutive levels of an H_2O_2 -enhanced phenol oxidase in vitro. This enzyme may be a lignin-degrading enzyme similar to the one found in the decay fungus *Phanerochaete chrysosporium* Burds (Tien and Kirk 1984).

This ability of *Armillaria* to decay wood after it has penetrated and killed the cambial tissues allows the fungus to maintain itself in woody tissues. Here it may build up inoculum potential and overcome the resistant reactions in the living cambial zone tissues, or infect and kill additional tissue when the tree is weakened by stress (fig. 3.9).

Host Factors

Physical barriers probably slow the penetration and infection of root tissue by *Armillaria*, but they do not prevent infection. Resistance is therefore mostly chemical as either preformed constituents in the bark or as mobilized constituents in response to penetration by the fungus. Limited work by Wargo (1984a) indicated that no increase in concentration of total or specific phenols occurred in bark tissues contiguous with bark naturally colonized by *Armillaria* or wounded and inoculated with the fungus. Since total bark was analyzed, the increase in phenols may have been masked. Other work indicates that phenol accumulation in bark tissue in response to fungal colonization occurs primarily in the inner bark regions (Ostrofsky and others 1984, Wargo 1988).

Preformed phenolics and other constituents can probably act as effective chemical barriers to penetration and infection by *Armillaria*. In vitro studies with *Armillaria* have shown that some phenols commonly found in both coniferous and deciduous hosts can inhibit fungus growth. Fifteen North American isolates representing at least the four species *A. mellea*, *A. gallica*, *A. ostoyae*, and *A. sinapina* (Wargo unpubl.) were challenged with hydrolyzable tannin (tannic acid, gallotannin) and gallic acid (Wargo 1980a). The isolates were both stimulated and inhibited depending on the phenol, the concentration of glucose, and the presence or absence of ethanol in the growth media (fig. 3.10). In general, gallic acid was more inhibitory to growth while hydrolyzable tannin was more stimulatory compared to the control. The ability to oxidize the phenolics seemed to be the key to inhibition or stimulation. Growth was inhibited if the isolate could not or only slightly (as determined by browning of the medium) oxidize the phenol. Growth was stimulated greatly where oxidation occurred readily; oxidation was initiated or accelerated by the addition of glucose and etha-

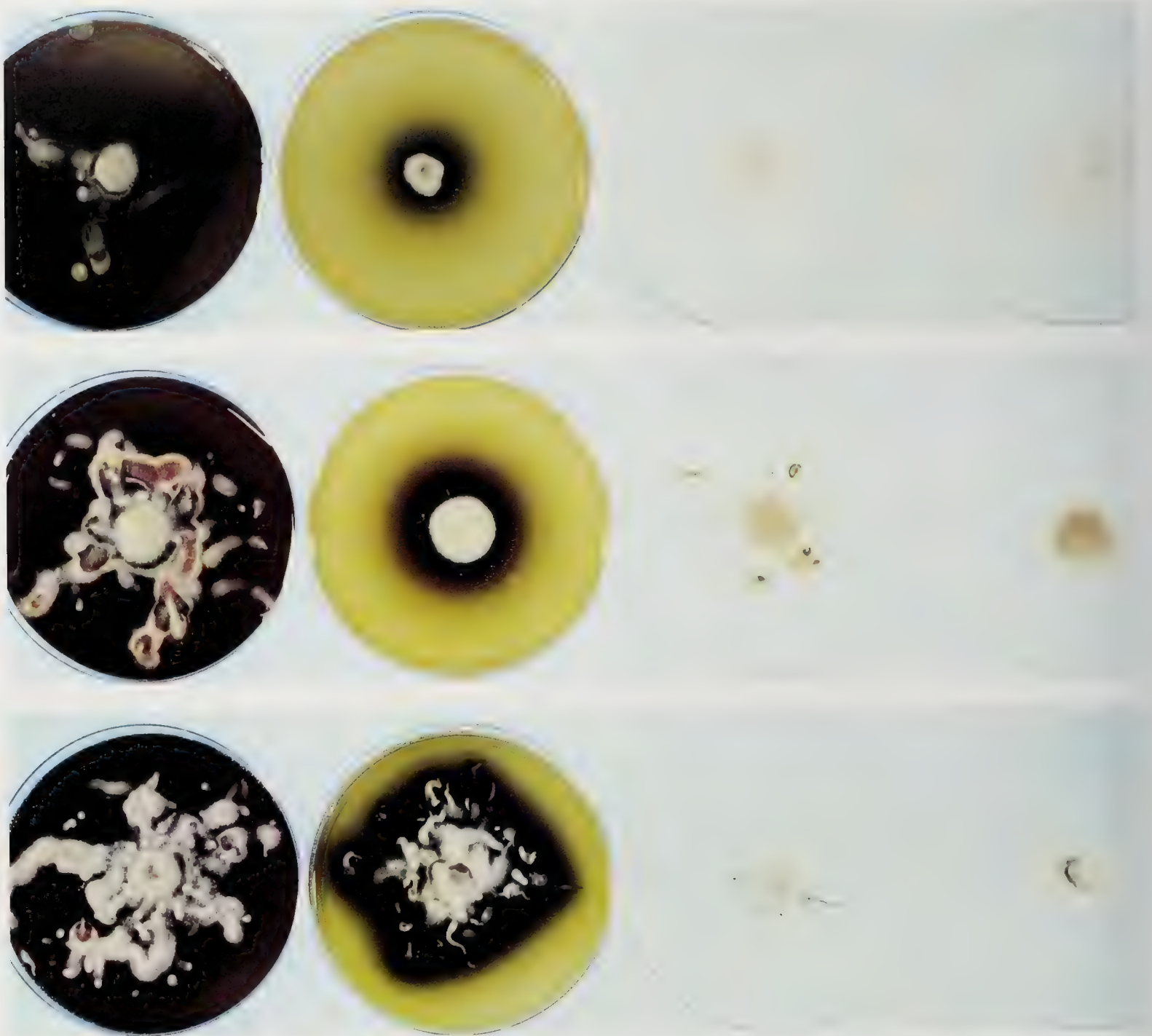


FIGURE 3.10 — Growth of an *Armillaria* isolate on gallic acid (GA) and control (C) media amended or not amended with ethanol (ET) and with three glucose levels (left to right, GA+ET,

GA, C+ET, C). Top: 1 g glucose/l; Middle: 5 g glucose/l; Bottom: 10 g glucose/l. (P. Wargo)

nol. Isolates of *A. gallica* oxidized gallic acid and grew better in its presence with or without ethanol than did isolates of *A. ostoyae*.

Wargo (1981d) also observed that some ponderosa pine isolates of *A. ostoyae* from the Western United States that were pathogenic on the pine (Shaw 1977) could not oxidize gallic acid and did not grow at all on malt agar amended with 0.5% (w/v) gallic acid. Some less pathogenic hardwood isolates (probably *A. gallica*, which are able to oxidize gallic acid and respond better to eastern hardwood isolates that better stress has altered the tree (Shaw 1985). Shaw (1985) could not confirm

these reactions to gallic acid. He found that gallic acid both with and without ethanol inhibited most (20/21-dry weight, 21/21-colony diameter) of the 21 *Armillaria* isolates tested representing *A. mellea* (4), *A. ostoyae* (4), *A. gallica* (5), NABS V (3), *A. luteobubalina* (3), and *A. novae-zelandiae* (2). Variation within a species was as great as among the species. Growth of all isolates was stimulated on tannic acid medium (hydrolyzable gallo-tannin) without ethanol; with ethanol, a few isolates (4/21) grew less.

The different response of *A. ostoyae* isolates to gallic acid in both studies (Shaw 1985, Wargo 1981d) may have resulted from the different inocula used. Wargo

used inoculum growing on water agar and Shaw used inoculum from 3% malt agar. The isolates on malt agar may have been conditioned to produce laccase (malt agar turns brown when *Armillaria* isolates grow in it, indicating oxidase activity) and were able to oxidize some gallic acid immediately. Also, Shaw amended 3% malt agar with gallic acid while Wargo used 2% malt agar. The difference in nutrient concentration could have affected the abilities of the various isolates to oxidize gallic acid (Wargo 1980a). Cheo (1982) also observed a carbohydrate effect on *Armillaria* growing on tannin-supplemented media. Growth of a single isolate with 0.5% tannin was 1.5 to 5 times greater when glucose was added to the medium.

The stimulation of *Armillaria* species by tannic acid and the inhibition by gallic acid suggests that the concentration of gallic acid and the rate at which it can be oxidized controls the response of the fungus. Tannic acid has approximately one glucose molecule for every five gallic acid molecules. The fungus may hydrolyze tannic acid to gallic acid, which it then oxidizes and polymerizes immediately. This prevents the gallic acid concentration from becoming inhibitory. Alternatively, the fungus may oxidize the tannin without hydrolyzing it, thus preventing gallic acid from building up in the substrate. No work has been conducted on degradation of tannins by *Armillaria*. Analyses of phenols and tannin degradation in oak bark tissues colonized by *Armillaria* showed that gallic acid did not occur in colonized tissue (Wargo 1984a). Gallic acid and various polymers (di, tri, etc.) of gallic acid were present in the healthy and discolored tissues contiguous with the colonized portion but these materials decreased in the colonized bark compared to healthy tissues. This suggests that *Armillaria* oxidizes tannic acid and other polymers of gallic acid but does not hydrolyze them to gallic acid. However, this needs to be verified with more critical experiments.

The ability of *Armillaria* to oxidize gallic acid, tannic acid, and other phenols in bark tissues is also influenced by carbon and nitrogen concentrations (Wargo 1983b). The growth rate and hence oxidation rate of phenols in extracts from root bark of black oak depended on supplemental glucose and nitrogen. Growth was directly proportional to the decrease in level of total phenols in a culture medium, and was five times greater in the phenol plus supplement medium than in supplement alone.

Phenols other than gallic acid and gallotannins also can inhibit *Armillaria* species. Both *A. ostoyae* and *A. gallica* were inhibited by various monophenols and alpha pinene, a terpene in conifer resins (Entry and Cromack 1989). Low levels of these phenols (<1 mg g⁻¹) stimulated rhizomorph production. No differences occurred

between the two *Armillaria* species in response to the various phenols or pinene; variation of growth response to each compound was as great within as between species. These results must be accepted very cautiously because the compounds were dissolved in 50 ml ethanol and added to 1 l of medium. This concentration of ethanol is 30 to 100 times greater than concentrations used in other studies. Results could be confounded by these high concentrations. Alkaloids are also known to inhibit *Armillaria*. Greathouse and Rigler (1940) found that alkaloids from several plant families inhibited growth of *Armillaria* in vitro.

Other plant constituents have been found highly stimulatory to *Armillaria*. Lipids from roots of ponderosa pine, Douglas-fir, white fir, incense-cedar, and peach promoted vigorous growth in vitro of an *Armillaria* isolate from California, probably *A. mellea* (Moody and Weinhold 1972a,b). The fatty acid fraction of the lipids was the active portion. Resin acids from ponderosa pine also were highly stimulatory and promoted twice as much rhizomorph growth as the fatty acid fraction from the same amount of root tissue. Abietic acid, a commercially available resin acid, stimulated rhizomorph production when it was sterilized by autoclaving but not by filtration, suggesting that breakdown products of the acids are the stimulatory factors. Fresh or autoclaved wound resin from ponderosa pine also stimulates in vitro growth of *Armillaria* (Shaw 1975) and has been used in medium prepared for cultural pairing tests (Shaw and Roth 1976).

Predisposition Effects

Stress

Susceptible or resistant responses of the host to a fungal pathogen depend on the genetic makeup of the host and the pathogen, and the environment in which they exist. Stress can alter the relationship and change the balance in the interaction between host and pathogen, resulting in root disease.

Stresses obviously affect the pathogen, but few studies report on these effects. We know that drought and waterlogging sometimes increase the incidence and severity of *Armillaria* root disease (see chapter 7). However, we have no idea how drought or waterlogging affect the fungus when it occurs as rhizomorphs in the soil or as mycelium inside tree tissues. For example, we do not know how turgor pressure in the rhizomorph influences penetration of the root bark; nor do we know how moisture extremes influence this relationship. Nechleba (1915), in his conclusions regarding the pathogenic relationship of trees and *Armillaria*, specu-

lated that dry conditions in forests promoted infection and colonization by inducing rhizomorphs of the fungus to colonize other substrates for water and nutrients. He proposed that the rhizomorphs "find their way instinctively (hydrotropism) toward living roots" and colonize them.

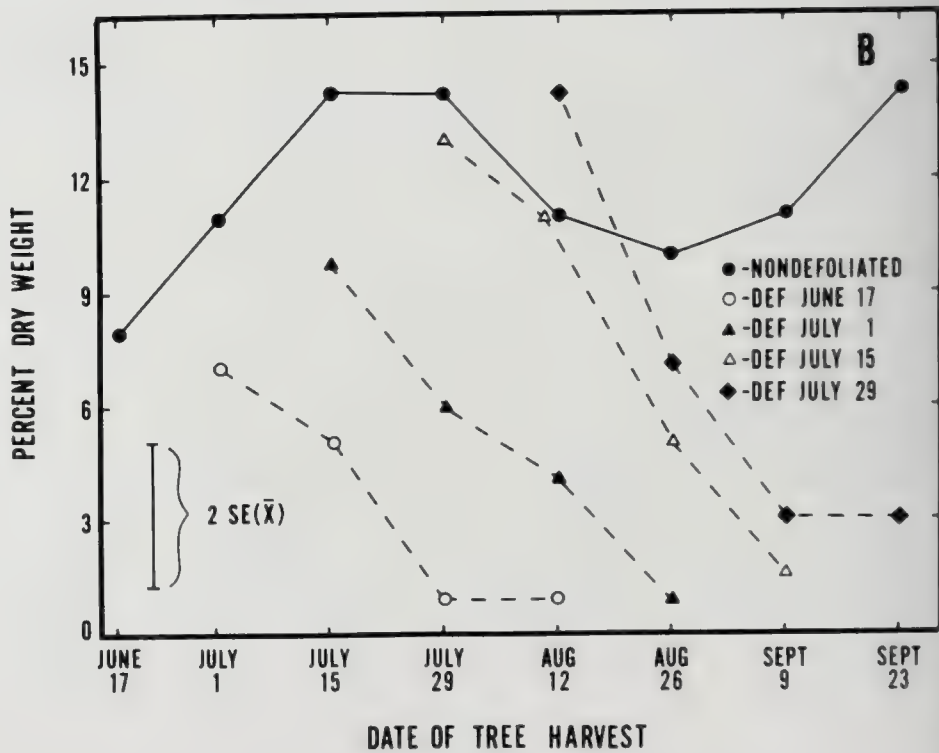
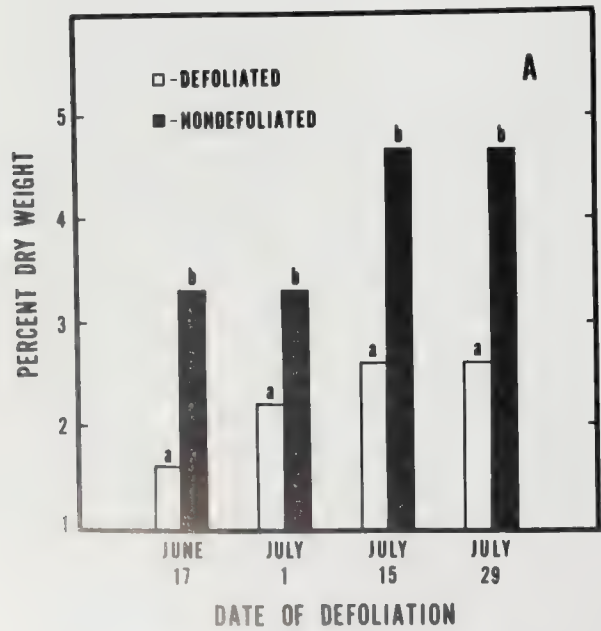
Armillaria species infect roots of healthy trees by rhizomorph contact, from diseased tissue, or by direct mycelial contact from diseased roots (see chapters 4 and 6). Hyphae penetrate the outer bark and "challenge" the inner bark tissue; it is here where stress influences the reaction. Chemical changes induced in the host by stress may promote susceptibility by (1) removing fungal inhibitors, (2) releasing nutrients and metabolites required by the fungus for pathogenesis, (3) providing the fungus with growth stimulators that allow it to overwhelm the capacity of the host root system to resist harmful fungal metabolites, or (4) reducing the capacity of the host tissues to tolerate or control the metabolites produced by the fungus (Wargo 1984b). All or any combination of these relationships may occur.

Many stresses predispose trees to *Armillaria* and initiate root disease or accelerate root disease in the host (see chapter 7). However, our knowledge about how stress specifically affects the relationship between *Armillaria* and its hosts is mostly about the host and is limited

predominantly to the effects of drought and insect damage on a few host tree species (Wargo 1983a,b; 1984a,b).

Nutritional Changes

Both drought and defoliation affect the carbohydrate and nitrogen levels in the root tissues colonized by *Armillaria* (Gregory and Wargo 1986, Parker 1979, Parker and Houston 1971, Parker and Patton 1975, Wargo 1972, Wargo and others 1972). Defoliation can substantially decrease the starch content in the root wood (fig. 3.11) and decrease sucrose levels in both bark and cambial tissues of sugar maple roots (Wargo 1972, 1981b). Reducing-sugar levels increase especially in cambial zone tissues. Concentrations of reducing-sugar can be 4-5 times higher in defoliated trees than those in non-defoliated trees at the same time of the year, and 3-4 times higher than the normal spring high when carbohydrates are mobilized for growth (Wargo 1971). Since *Armillaria* predominantly uses glucose (Garraway 1975, Wargo 1981a), this increase is potentially important to the fungus. Growth on glucose or polymers of glucose, such as maltose and starch (fig. 3.12), can be 1.5-3 times higher than growth on other carbon sources (Wargo 1981a). Enhanced growth of *A. calvescens* (Wargo unpubl.) on root extracts of defoliated sugar maples was related to higher levels of glucose in the extract (Wargo 1972).



Decline in sucrose and starch content in the sugar maple roots caused by defoliation. A:

Sucrose level in the inner bark; B: Starch level in wood. (From Wargo 1972)

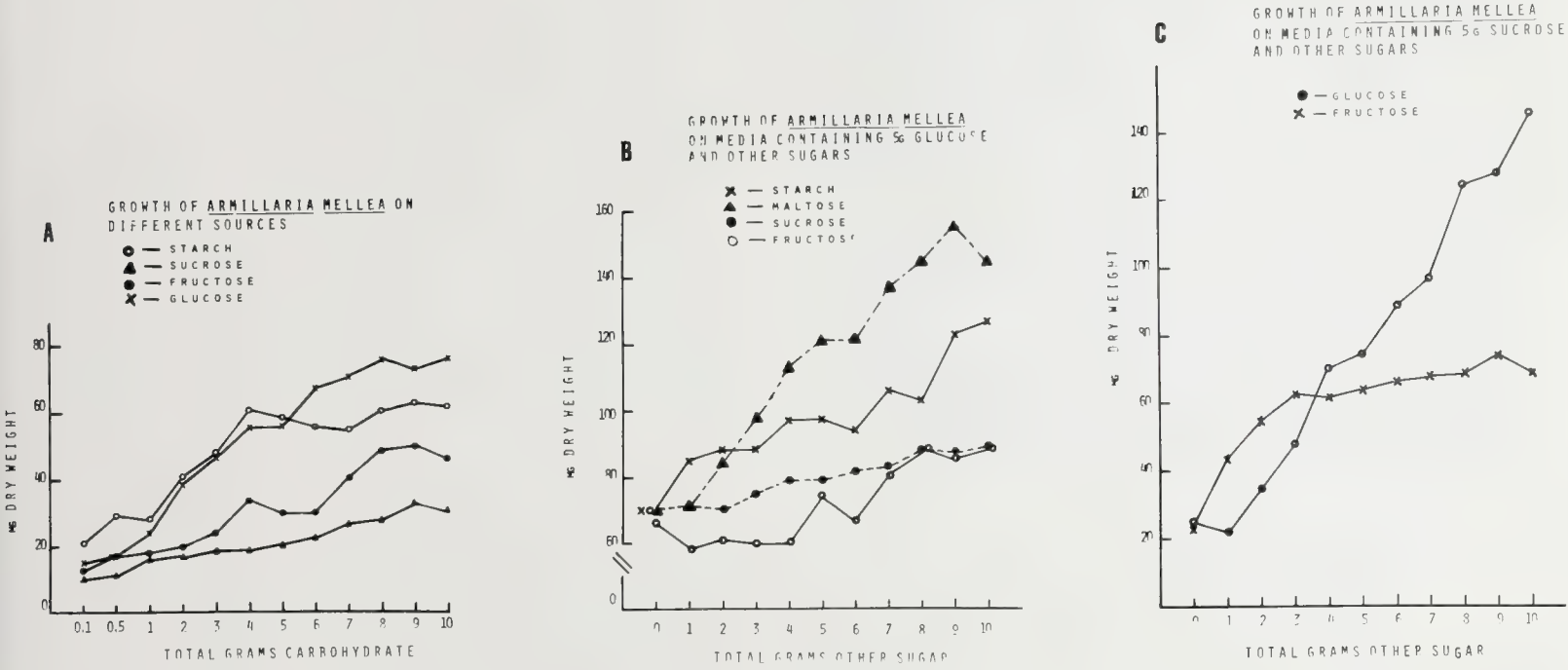


FIGURE 3.12 — Growth in vitro of *Armillaria* on various carbohydrates that demonstrate the stimulation of growth by glucose. A: Growth on various carbohydrates; B: Growth on

glucose media supplemented with various carbohydrates; C: Growth on sucrose media supplemented with glucose and fructose. (From Wargo 1981a)

Drought and defoliation also increase both total amino nitrogen levels and certain individual amino acids in sugar maple trees (Wargo 1972) and seedlings of black and red oak (Parker 1979, Parker and Patton 1975). Both individual amino acids and total amino nitrogen supplements were very satisfactory nitrogen sources for in vitro growth of *Armillaria* (Weinhold and Garraway 1966), as discussed previously.

Also, noted earlier, ethanol is a potent stimulator of *Armillaria*, especially rhizomorph production and growth (Weinhold 1963, Weinhold and Garraway 1966). In the presence of ethanol, the fungus can metabolize phenolic compounds that would otherwise inhibit growth (Longworth and Garraway 1981; Wargo 1980a, 1981d). Ethanol enhances laccase production by the fungus (Worrall and others 1986) and improves its ability to utilize carbon sources other than glucose (Weinhold and Garraway 1966).

Ethanol could be an important factor in stressed trees. Stress from flooding or defoliation can stimulate ethanol production and accumulation in woody roots (Wargo unpubl.). On poorly drained sites and more mesic areas, seasonally high water tables often occur and cause anaerobic conditions about tree roots. Defoliation, because it reduces transpiration, promotes or

prolongs wet soil conditions. In oak forests in Connecticut, soils in stands defoliated by the gypsy moth (*Lymantria dispar* L.) were wetter and defoliated trees contained more water than soils and trees on adjacent nondefoliated sites (Stephens and others 1972). Significant amounts of ethanol can be produced in roots depending on the duration of the anaerobic conditions and tree species (Coutts and Armstrong 1976, Crawford and Baines 1977). Injection of ethanol into roots of black and white oaks promoted colonization of the roots by *Armillaria*. Colonization, however, was related more to tissue necrosis caused by the ethanol rather than to the ethanol alone (Wargo and Montgomery 1983).

Phenol Degradation

Stress-induced chemical changes in roots may also determine how well *Armillaria* can oxidize phenols. Inhibition of *Armillaria* growth by gallic acid was lessened or reversed by adding more glucose to the medium (Wargo 1980a). Growth in bark extracts from black oak roots depended on phenol oxidation, which was greatly enhanced by adding glucose and nitrogen to the extract (Wargo 1983b). Additional growth studies using commercial sources of phenols found in oak bark (quercetin, quercitrin, catechin, and tannic acid) indi-



FIGURE 3.13 — Growth of an *Armillaria* isolate on an extract from red oak bark. Upper flask—extract + glucose + ethanol. Lower flask—as above + 500 ppm ascorbic acid. (P. Wargo)

cated that if the fungus could oxidize the phenol, the phenol no longer inhibited the fungus (Wargo unpubl.). Growth was also stimulated, suggesting that the oxidized phenols were being utilized as carbon sources or growth regulators. If oxidation of the phenols were inhibited by adding a reducing agent (fig. 3.13), growth significantly declined (Wargo unpubl.).

Successful colonization of root tissues in stressed trees may depend on the fungus' ability to oxidize phenols and the inability of the tree tissue to prevent the oxidation reaction. In healthy deciduous trees, *Armillaria* appears to be confined to wounded and necrotic tissue; contiguous healthy tissues are not "browned" or colonized by the fungus. In weakened trees, contiguous living tissues are "browned" in advance of the fungus, probably by extracellular secretions of laccase and peroxidase, and then colonized (Wargo 1983b, 1984a). This interaction has similarities to that proposed for the redox theory of hypersensitivity reaction (Goodman and others 1986) where necrosis in response to fungal invasion occurs when the balance between reductive and oxidative processes shift in favor of the latter. In healthy tissues, necrosis induced by *Armillaria* is inhibited or contained, probably by a highly reductive state in contiguous tissues. Perhaps stressed tissues cannot confine the oxidative processes and necrosis begins and spreads as oxidative and other enzymes are secreted by the fungus.

Host-Induced Lysis

Host-produced enzymes that may potentially assist bark tissue in resisting *Armillaria* are also affected by stress from defoliation (Wargo 1976). The hyphal walls of *Armillaria* contain chitin and beta-1,3-glucan, and are vulnerable to lysis by chitinase and beta-1,3-glucanase (Ballesta and Alexander 1972, Bouveng and others 1967, Wargo 1975). These enzymes are found in bark and sap of several oaks and sugar maples, and their activities are lowered by defoliation (Wargo 1975, 1976). Lysis of *Armillaria* hyphae in vivo has been reported for species associated with orchids (Hamada 1940, Kusano 1911) and the description of fungal digestion in orchid species suggests a host-mediated lysis (Burges 1939).

Complete dissolution of the hyphae is not necessary to disrupt growth. Hyphal tips grow by a delicate balance between wall synthesis and wall lysis, and bursting of the hyphal tips can occur when the balance shifts toward the lytic stage (Bartnicki-Garcia and Lippman 1972). Extrahyphal enzymes in host cells that can dissolve hyphal wall components could alter the wall formation balance, disrupt hyphal-tip growth, and provide a defense mechanism against invasion by fungal pathogens. More recent work on these enzymes indicates that they are indeed potent inhibitors of fungal growth (Schlumbaum and others 1986).

The fungus is not defenseless against lysis by host-produced enzymes. The phenol oxidase enzymes, especially tyrosinase, produced by the fungus are linked to melanin synthesis by fungi (Mayer and Harel 1979). As noted earlier, *Armillaria* is capable of producing melanin-like pigments in rhizomorphs and probably to a limited extent in hyphae (Chet and Hüttermann 1977, Smith and Griffin 1971). Phenol oxidase-catalyzed formation of extracellular pigments may be related to the formation of melanin-like pigments in hyphae. They may strengthen hyphae (Bell and Wheeler 1986) and protect them from dissolution by lytic enzymes (Bloomfield and Alexander 1967).

Conclusions

Host-pathogen interactions ultimately depend on the relationship of fungal species, host species, and the environment in which they interact, including the disturbances induced by stress. Much of the information on the physiological and chemical interactions of *Armillaria* species and their hosts is fragmented, and the characteristics of the events for any one species of

Armillaria and its host are incomplete. The fungus penetrates generally through intact bark, interacts with the inner bark, is stimulated to colonize and kill the inner bark, and either invades the cambial zone or is inhibited by as yet unknown mechanisms. The interaction with phenols present in the bark tissues is probably a major event in determining resistance or susceptibility and the pathogenic process. Stress from a variety of sources influences the resistance mechanisms and enhances penetration, colonization, and killing by *Armillaria*.

The concepts discussed in this section are based on fragments of information concerning the many interac-

tions that can occur among the many *Armillaria* species and host species. Studies using clonal host material, known species, and genotypes of *Armillaria* and stressed and non-stressed systems must be conducted to elucidate the kinds and sequence of pathogen and host changes that occur in resistant and susceptible reactions. Some of the morphological and anatomical interactions have been characterized. These must be verified in the host-pathogen system described above, and the chemical changes associated with these interactions must be characterized. This area of research is ripe for much work by the students of host and fungal physiology and their interactions.

Inoculum and Infection

Derek B. Redfern and Gregory M. Filip

All *Armillaria* species survive saprophytically in woody substrates in soil, and the majority form the most highly organized rhizomorphs of any fungus. By extension of these rhizomorphs through the soil, the fungus can colonize additional woody material. Varying degrees of pathogenicity may be exhibited during this phase. Robert Hartig (1873b) was the first to not only make the link between the spread of infection and the presence of nearby trees previously killed by the fungus, but also to suggest that rhizomorphs cause infection.

Descriptive terms such as "food base" and "invasive potential" have obvious application to the rhizomorph-forming *Armillaria* species. "Inoculum potential" is a similar term. This concept was explored by Garrett (1970), partly through a series of experiments with *A. mellea* (*sensu lato*) (Garrett 1956b). The term was not new, but he redefined it (1970) as "the energy of growth of a parasite available for infection of a host, at the surface of the host organ to be infected." The definition encompasses the net effect of variables such as the surface area of fungus in contact with unit area of host, the vigor of the invading hyphae, and environmental effects on the fungus.

This chapter deals primarily with factors that affect the success of infection through their effect on inoculum potential. First, the nature of the inoculum capable of causing infection and the quality of the substrate provided by different tree species are considered. The second part concentrates on those factors which affect the success of infection through their effect on the fungus, particularly the rhizomorphs, which provide the means of infection and spread in most *Armillaria* species.

Inoculum

Source of Inoculum

For most purposes, wood provides the only effective medium from which *Armillaria* can spread and

cause infection. Tree roots constitute the major source of inoculum, but logging debris may also be colonized and act in the same way (MacKenzie and Shaw 1977).

The fungus becomes established in roots and stumps by infecting live trees and by colonizing stumps created during felling operations. If a tree is killed, the entire root system may become inoculum. The fungus colonizes newly created stumps in three ways: by rapid extension from pre-existing lesions in which it was formerly held in check by host resistance (Kile 1980b, Leach 1939); by invasion from an epiphytic position on the roots; or by invasion from outside by newly arrived rhizomorphs.

Based on Garrett's work (1960, 1970), the series of circumstances under which *Armillaria* becomes established in substrates can be taken to represent a requirement for a decreasing parasitic ability and an increasing competitive saprophytic ability. Logging residues constitute an extension to the series because, apart from being less readily available for colonization than stumps by virtue of position, their tissues are likely to die more rapidly and be available earlier for colonization by competing saprophytic organisms.

Where stumps provide potential sources of inoculum, they are most commonly colonized by vegetative spread, but the cut surface can also provide an avenue for colonization by basidiospores (Rishbeth 1970, 1978b, 1988). A number of researchers have failed to infect stumps in this way, however (Kile 1983b, Leach 1939, Podger and others 1978), while others have had very limited success (Swift 1972). It is apparently an uncommon event but may be important to disease development in certain crops (Horner 1988). Even though basidiospore-infected stumps probably constitute a minor portion of the total inoculum, spore infection is important for providing a source of genetic diversity, for facilitating long-range spread, and also for infecting forests established on arable land. Some work on genotype identification (Hood and Sandberg 1987, Horner

1988, Kile 1983b, Ullrich and Anderson 1978) provides indirect evidence for spore infections, but similar work by others provides less support (Shaw and Roth 1976).

No evidence indicates basidiospores can directly infect living roots, presumably because the inoculum potential provided by the limited resource within spores is inadequate. Hartig (1874) suggested that basidiospores may colonize dead organic matter and subsequently form rhizomorphs, but no experimental evidence supports this.

In experiments, most successful infections have been achieved using woody inocula prepared either from naturally infected roots (Leach 1937) or by culturing the fungus in various ways on woody stem or root segments (Patton and Riker 1959, Redfern 1975, Shaw 1977, Thomas 1934). Cultures established on non-woody substrates such as nutrient agar, bran, or bean pods have been generally unsuccessful as inocula (Bliss 1941, Plakidas 1941). Wood is not an absolute prerequisite for infection; inocula derived from less substantial substrates may be adequate. For example, Guyot (1927) caused infection using cultures on an agar medium containing acorns and horse chestnuts. Nevertheless, only a woody substrate is able to provide an inoculum which is sufficiently durable and potent to cause disease reliably.

Under experimental conditions, infection has been achieved even without a substrate by means of excised rhizomorphs. These pieces can be large enough to form new growing tips with an inoculum potential high enough to infect healthy seedlings (Redfern 1973, Rykowski 1984). Holdenreider (1987) caused infection in a similar way but found wounds to be an apparent prerequisite. Other reports concerning the infective potential of detached rhizomorphs have been negative (Bliss 1941).

In common with other root-rot fungi, *Armillaria* inoculum is generally confined to infested sites. However, roots may become fragmented and transported by water, thus potentially creating new foci of infection (Hewitt 1936). Colonized logging debris could be transported in the same way. The rhizomorph-forming ability of most species would enable *Armillaria* to exploit such an event much more effectively than other root pathogens such as *Heterobasidion annosum* (Fr.) Bref. and *Phellinus weirii* (Murr.) Gilbn.

Substrate Quality—Conifers Versus Hardwoods

Armillaria mellea sensu lato was considered to be a highly variable species long before the present understanding of speciation in the genus and of the ecology

of these species. In spite of this, much of the observed variation in disease was attributed to factors other than variation in pathogenicity. Prominent among these was the nature of the substrate providing the inoculum.

Disease is now known to be associated with stumps of many species, ranging from Australasian hardwoods (Kile 1981, Podger and others 1978, Shaw and Calderon 1977) to European and North American conifers (Redfern 1975, Shaw and others 1976a). Early records, however, largely associated mortality with hardwood stumps. A possible reason for this is that until relatively recently the disease attracted most attention in fruit orchards and in plantations of tea, coffee, rubber, and exotic conifers, all established on land cleared of indigenous forest where *Armillaria* was endemic. In the tropics and sub-tropics, this original forest comprised a mixture of broadleaved species (Leach 1939). In temperate regions, hardwoods would probably have been at least a major component on the richer soils where such plantation crops were grown. Many early reports of disease concern losses in these circumstances (Butler 1928, Dade 1927, Gibson 1960, Hendrickson 1925, Horne 1914, Lawrence 1910, Nechleba 1915, Rhoads 1956, Wallace 1935). In California, the disease occurred so consistently in orchards planted on land cleared of oaks that for many years articles in Californian agricultural journals referred to *Armillaria* as the “oak root fungus” (Kimball 1949, Raabe and others 1967).

In Europe, Hartig (1874) and Nechleba (1915) observed that serious disease may occur where conifer plantations replace hardwoods, whereas damage is generally unimportant in crops replacing conifers. This had a major influence on early thinking about how substrate affects disease development. The prevailing view was that hardwood stumps provide a superior substrate to conifer stumps. Peace (1962), for example, commented that *Armillaria* is essentially a fungus of areas with a hardwood history, and suggested that where conifers replace hardwoods damage is likely to be absent or much reduced in the second conifer rotation. During the first rotation, conifer stumps left after thinning are readily colonized by *Armillaria* (Greig 1962, Low and Gladman 1962), but Peace (1962) believed the fungus acts purely saprophytically in this situation and there is no increase in parasitic activity. The implication was that conifer stumps have little or no significance in sustaining attacks.

By contrast with observations implicating hardwood stumps as sources of infection, the first reports in which disease was clearly identified as being associated with conifer stumps are relatively recent. Weiss and Riffle (1971) recorded killing of ponderosa pine following a crop of the same species, and Swift (1972) reported losses in slash pine planted as a second rotation

on a site formerly occupied by indigenous hardwoods. Ono (1965, 1970) and Redfern (1975) reported serious disease where the major source of nutrition for the fungus was provided by conifer stumps. Initially, such observations were rare among the continuing reports concerning hardwoods (Gladman and Low 1963, Huntly and others 1961, MacKenzie and Shaw 1977, Ono 1965, Pronos and Patton 1978, Swift 1972). They have become more numerous, particularly from natural coniferous forests in North America (Morrison 1981, Wargo and Shaw 1985), as increasing interest in forest management draws attention to the impact of *Armillaria* losses. In the Northwestern United States, conifer stumps were shown to be effective inoculum sources (Filip 1979, Roth and others 1980) causing considerable infection and mortality in several indigenous coniferous species, especially in partially harvested forests (Filip 1977, Filip and Goheen 1984, Shaw and others 1976a).

In experiments, trees have been successfully infected using inocula prepared from stems and roots of various coniferous and hardwood species, providing ample evidence of at least the short-term suitability of coniferous substrates as food bases for *Armillaria*. Species used include red pine and eastern white pine (Patton and Riker 1959); Japanese larch (Ono 1970); fig and citrus (Wilbur and others 1972); common beech, planetree and Scots pine (Redfern 1975, 1978); Sitka spruce (Singh 1980a); alder (Shaw 1977, Shaw and others 1981); and English oak (Morrison 1982b).

While rhizomorph production may not be the best measure of substrate quality, particularly for those pathogenic species which produce few rhizomorphs, it has been commonly used. Thus, in experiments to determine the relative value of the substrate provided by roots of hardwood and coniferous species, Redfern (1970) found that segments of red maple inoculated with *Armillaria* produced a greater number, total length, and dry weight of rhizomorphs than red spruce segments of equal volume. However, when corrections were made for differences in initial wood density of the two species, differences in length and weight were no longer evident, although maple segments still produced a greater number of rhizomorphs than spruce. Working with several *Armillaria* isolates and several coniferous and hardwood species as substrates, Morrison (1972) found that, with the exception of one isolate, hardwood segments produced a greater dry weight of rhizomorphs than conifer segments. He made a similar comparison for density. The number of rhizomorphs was similar in this experiment, but when stumps were used in the field, Morrison found that the number of rhizomorphs, as well as the total length of rhizomorphs per stump, was greater for hardwood than conifer stumps. In a similar study,

which included measuring rhizomorph production by naturally infected stumps, Rishbeth (1972b) concluded that pines are inferior to English oak as substrates for *Armillaria* in terms of the number and weight of rhizomorphs produced. In comparing maritime pine with oak, Guillaumin and Lung (1985) obtained the same results as Rishbeth for both *A. ostoyae* and *A. mellea*.

Redfern (1975) examined the effect of substrate on infection as well as rhizomorph production. Sitka spruce seedlings were inoculated with four isolates of *Armillaria* growing on root segments of either planetree or Scots pine. Gregory (1985) subsequently identified these isolates to species. *Armillaria ostoyae* and *A. mellea* killed more trees when growing on planetree than on pine, whereas the reverse was true for *A. gallica*. Substrate species had no effect on *A. cepistipes*. Rhizomorph production was significantly greater on planetree than on pine for three of the species (*A. ostoyae*, *A. gallica*, and *A. mellea*), but *A. cepistipes* produced more on pine. *Armillaria ostoyae* and *A. mellea* were both highly pathogenic in the experiment, whereas the other two species showed very low pathogenicity. Thus, for both pathogenic species, rhizomorph production and infection were favored by a hardwood rather than a coniferous substrate. Rykowski (1984) obtained similar results in experiments with Scots pine seedlings and inocula prepared from branch segments. Hardwood substrates, especially oak and common beech, were superior to Scots pine and European larch for both rhizomorph production and infection. Three isolates were used, but only one produced rhizomorphs consistently and caused infection. The species was referred to as *A. mellea*, but evidence in the paper suggests it was *A. ostoyae*.

In similar work with the Australasian species *A. novae-zelandiae* and *A. limonea*, Benjamin and Newhook (1984b) ranked a number of indigenous and exotic hardwood species and two exotic conifers, radiata pine and ponderosa pine, as substrates for rhizomorph production. The two conifers occupied an intermediate position among the hardwoods as food bases for *A. novae-zelandiae*, whereas they were equal or superior to most of the hardwoods for *A. limonea*. Interestingly, the native hardwood tawa provided the best substrate for both species. In pathogenicity trials using the two *Armillaria* species with radiata pine and eucalypt seedlings, radiata pine and several hardwood food bases were equally effective substrates when tested against radiata pine seedlings. Some evidence indicated that tawa was superior to radiata pine against eucalypt seedlings.

Pearce and Malajczuk (1990a) tested the quality of the food base provided by two common hardwood hosts of *A. luteobubalina* by measuring rhizomorph production.

They found that stem segments of sunbush were superior to those of karri. Three genotypes of *A. luteobubalina* behaved in the same way.

With so few experiments on substrate quality, data are insufficient to suggest a general superiority of one wood type over the other as a food base, but some *Armillaria* species or isolates may be favored by particular species. However, observations similar to those made by Nechleba (1915) concerning the association of killing attacks with former hardwood sites continue to be made (Rishbeth 1982, Rykowski 1984). In the field, factors other than the intrinsic quality of the substrate may determine a stump's effectiveness as an inoculum source. Morrison (1972) and Rishbeth (1972b) both concluded that the frequently reported association of hardwood food bases with disease could be partially attributed to those broadleaved trees in which resistance to infection is maintained by regrowth after cutting. They are less quickly exhausted as food bases than conifer stumps, which die rapidly. The generally higher wood density and greater resistance to decay of hardwood species compared to conifers (Rykowski 1984) may also increase the longevity of hardwood inocula.

The possible "field" superiority of hardwood food bases as inoculum, at least for some *Armillaria* species, is not great, and the association of disease with hardwood stumps should not be over-emphasised. As discussed by Redfern (1975), it may be a mistake to assume that damage will diminish appreciably in succeeding conifer rotations. This is supported by recent survey data from second-rotation radiata pine stands established on land cleared of indigenous hardwood forest (MacKenzie and Self 1988). It is salutary to quote Hartig, who wrote in 1874: "The disease often occurs especially destructively where the planting of conifers has been carried out after the felling of hardwoods But it should not be maintained from this that the rhizomorphs attack only from hardwood stumps to the conifer woods since, as we said earlier, the mycelium grows for several years on all conifer stumps and roots; therefore, hardwood stumps are not necessary for the spread or origin of the disease."

The nature of the substrate probably has far less direct influence on disease development in plantations than the pathogenicity of the *Armillaria* species present in the previous crops. However, an indirect substrate effect may occur through species selection resulting from host specialization. Thus, Rishbeth (1985a) found that despite being rare on broadleaved trees and stumps, *A. ostoyae* caused death as commonly as *A. mellea* in conifers established on sites previously occupied by broadleaved woodland. Where conifers replaced conifers, it was the predominant cause of mortality.

The importance of variation in pathogenicity between species is suggested in the early North American literature. In a notable paper, Piper and Fletcher (1903) described damage in prune orchards by two forms of *A. mellea* (*sensu lato*). One form, referred to as *A. mellea*, caused severe damage and was believed to have been introduced. The other, referred to as *A. mellea bulbosa*, was much less damaging. The latter was abundant on native trees, both conifers and hardwoods. Later, Childs and Zeller (1929) observed disease in apple orchards established on sites cleared of oak, but found no disease on sites formerly occupied by Douglas-fir. Both site types were infested with *Armillaria*, which the authors suggested might exist as two strains differing in "pathogenicity" (see chapter 6).

Substrate Specialization

In common with other wood-rotting fungi that kill tree roots, *Armillaria* is polyphagous. Individual species or isolates grow on excised stems or roots of many tree species, including ones which they would not encounter naturally (Benjamin and Newhook 1984b, Rishbeth 1978a). There is little *prima facie* evidence for substrate specialization. In the field, however, substrates are acquired both parasitically and saprophytically. Where several *Armillaria* species of different pathogenicity and competitive saprophytic ability are present in the same forest type, substrates are unlikely to be equally available to them all. Our knowledge of the better-known species clearly shows that their association with particular substrates reflects their ecology rather than a substrate specialization or preference.

Armillaria ostoyae is highly pathogenic and occurs mainly on conifers throughout Europe and North America (see chapters 6 and 8). However, its association with conifers is not exclusive. In Canada, Morrison and others (1985a) found that broadleaved trees within disease centers were frequently attacked and killed. Elsewhere in North America, *A. ostoyae* kills cherry (Proffer and others 1987) and several other hardwood species (Harrington and others 1989). By contrast, Europe's other major pathogenic species, *A. mellea*, may be described as a "hardwood species" because it has a wide host range among hardwood trees and shrubs, and is common on hardwood stumps (Guillaumin and others 1985, Rishbeth 1985a). The association is not exclusive, however, as it also attacks young or weakened conifers and occasionally occurs on conifer stumps (Davidson and Rishbeth 1988, Rishbeth 1985a). *Armillaria gallica* also has a wide host range (Guillaumin and others 1985) and has been recorded as a weak pathogen on both hardwood and coniferous hosts, but it is most important as a cause of butt rot in hardwood trees and as a colonist of hardwood rather than conifer stumps (Rishbeth 1985a). Morrison and

others (1985a) found *A. gallica* exclusively on living and dead hardwood hosts.

Experiments show that whereas only *A. mellea* and *A. ostoyae* infect vigorous English oak and Scots pine, respectively, all three species colonize both hosts when resistance is reduced by suppression (Davidson and Rishbeth 1988). Neither host specialization by the fungus nor selectivity by the tree are apparently maintained under these circumstances. Thus, for *A. ostoyae* and *A. mellea*, their host specialization as primary parasites largely determines their substrates as saprophytes.

Kile and Watling (1983, 1988) have discussed the ecology of the five known Australian species (see chapter 8). Four of these species, *A. luteobubalina*, *A. hinnulea*, *A. novae-zelandiae*, and *A. fumosa*, have extended geographical distributions which include Tasmania. *Armillaria hinnulea* and *A. novae-zelandiae* also occur in New Zealand. Some species overlap ecologically, but the last two species occur in wet forests, whereas *A. luteobubalina* predominates in dry sclerophyll eucalypt forests. *Armillaria fumosa* has only been found on wet sites within these dry forests, and is therefore associated with the particular species of these locations.

Armillaria luteobubalina is the only Australasian species for which comprehensive information about substrate specialization is available, but it does not indicate substrate specialization among the hosts commonly present in the dry sclerophyll eucalypt forest. Both stumps and trees of the major eucalypt species groups are equally susceptible to infection (Kellas and others 1987, Pearce and others 1986, Shearer and Tippet 1988); its host range includes 81 species in 21 plant families (see table 8.1).

In New Zealand, *A. limonea* and *A. novae-zelandiae* cause serious disease in radiata pine established on sites formerly occupied by indigenous forest comprising host species such as tawa and rimu (MacKenzie and Shaw 1977). However, no evidence indicates that certain species provide superior substrates or that they are preferred substrates for one *Armillaria* species or the other (MacKenzie and Shaw 1977, van der Pas 1981a).

In general, there is little evidence for substrate specialization within the natural range of each *Armillaria* species. The New Zealand example provides a dramatic illustration since the two species involved appear to have been transferred successfully from indigenous hardwood to introduced northern-hemisphere conifer (MacKenzie 1977). Nevertheless, in northern temperate forests, *Armillaria* species express a degree of specialization. *A. mellea* and *A. gallica* are generally found on living hosts and *A. ostoyae* with

The infection of stumps by basidiospores offers, in a sense, a "free choice" of substrate. Rishbeth (1988) made the interesting observation that *A. ostoyae* and *A. gallica* most frequently colonized conifer and hardwood stumps, respectively, although both species also colonized the other substrate.

Longevity of Inoculum and Persistence of the Fungus

Most estimates of inoculum longevity are based on observations made on single occasions, and refer to the ages of stumps which show evidence of viable *Armillaria*. Observations of this nature offer no information on the persistence of the fungus on the site and may underestimate its longevity in individual stumps. For example, survival in the stumps of hardwood trees showing regrowth may be greatly affected by the extended period over which such stumps become colonized. When the fungus is already present as a perthophyte or as a butt rot, colonization may begin long before the tree is felled. Thus, longevity of the fungus in individual roots may give little idea of the time over which the stump may act as an inoculum source.

Estimates vary widely but generally indicate fungal survival for decades in both broadleaved and coniferous stumps. Pronos and Patton (1978) found that oaks killed by herbicide produced rhizomorphs for at least 14 years, and Rishbeth (1972b) reported that wood from English oak stumps could do so 40 years after the trees were cut. Swift (1972) gave a figure of at least 20 years for survival in East African hardwoods. The only data available for conifers are from ponderosa pine in North America, and probably refer to *A. ostoyae*. Shaw (1975) found that wood cut from 30-year-old stumps contained viable *Armillaria* which could produce rhizomorphs; Roth and others (1980) isolated the fungus from large, old-growth stumps more than 35 years old. They estimated that it would remain viable in such stumps for at least 50 years. Few data are available for identified species. Kile (1981) suggested a longevity of 15-25 years for *A. luteobubalina* in messmate stringybark. In contrast, he isolated *A. hinnulea* from 70-year-old stumps of the same eucalypt species (Kile 1980b and pers. comm.). Rishbeth (1985a) recently reported an example in which *A. gallica* remained viable in an oak stump 53 years after felling.

Making valid comparisons between species based on field observations is difficult since longevity is likely to be affected by the stump species, its size, and by environmental factors. The difference in longevity between *A. luteobubalina* and *A. hinnulea* quoted above might be attributable largely to site differences since the observations were made in different forest types (G.A. Kile,

pers. comm.). There are some indications from experiments with small inocula about the effects on survival of soil moisture (Pearce and Malajczuk 1990a), temperature (Bliss 1946), and competing fungi such as *Trichoderma viride* Pers.: Fr. (Garrett 1957) but further work is required. Inoculum size may not be a major factor. Even in the comparatively minute inocula used in experiments, the fungus remained viable in Sitka spruce for at least 4 years (Singh 1980a) and in pine for up to 3 years (Patton and Riker 1959).

Armillaria can persist on a site for a very long time. For example, Shaw and Roth (1976) suggest that individual clones of *A. ostoyae* may survive for several centuries. Clearly this must involve a succession of substrates. For pathogenic species, these may be acquired either at the margins of expanding disease centers or among regenerating trees within disease gaps following a period of survival in stumps. The figures cited for longevity in individual stumps suggest this period may be sufficiently long to permit a resurgence of disease. For weakly pathogenic species, persistence may be aided by the behavior of the extensive rhizomorph systems some of them form.

In unmanaged forests, longevity probably confers a survival advantage on all species, but it may be particularly important for the less pathogenic ones since the opportunity for them to acquire additional substrates may be more limited than for more pathogenic species. The latter may benefit, particularly in forests of susceptible species, by survival in disease gaps until a new crop becomes established. In forests which are managed intensively and are subject to selection cutting or regular thinning, longevity may no longer be a survival trait, at least for weakly pathogenic species, since a regular supply of stumps would be available for colonization.

Factors Affecting Growth of Rhizomorphs from Inoculum

The abundance, type, and distribution of rhizomorphs on a site are primarily determined by the *Armillaria* species present, but environment exerts a major influence through the effects of soil.

Variation Among Species

Whereas all *Armillaria* species form rhizomorphs to some degree in axenic culture, not all have been observed to do so in the field. No rhizomorphs have been reported for *A. tabescens* (Rhoads 1956, Rishbeth 1982, Ross 1970) although Rishbeth observed them on inocula buried in soil. In *A. luteobubalina*, they are either absent (Kile 1981, Shearer and Tippet 1988) or sparse under natural conditions (Pearce and others 1986,

Podger and others 1978); other Australasian species, for example *A. limonea* and *A. novae-zelandiae* (Hood and Sandberg 1987), form rhizomorphs readily. *Armillaria hinnulea* forms rhizomorphs more prolifically than *A. luteobubalina*, but they are confined to root surfaces (Kile 1980b, Kile and Watling 1983). Among European and North American species, rhizomorph production is greater in *A. gallica* and *A. cepistipes* than in *A. ostoyae* and *A. mellea* (Gregory 1985, Guillaumin and others 1989a, Redfern 1975, Rishbeth 1985a). Information is lacking for some of the more recently described species such as *A. pallidula* and *A. fellea* (Kile and Watling 1988), but *A. sinapina* is reported to produce rhizomorphs abundantly in the field (Bérubé and Dessureault 1988). At the present time, information is insufficient to establish that the ability to produce rhizomorphs represents a continuum among species, but that may well be the case.

Morrison (1989) studied rhizomorph production by an array of species from Europe, Australasia, and North America using woody inocula buried in pots containing a mixture of forest soil, peat, and sand. While producing valuable information, such studies are not necessarily a reliable guide to field behavior. Thus, *A. luteobubalina* produced rhizomorphs more abundantly (fig. 4.1) under these circumstances than might have been anticipated from the field observations reported above. Podger and others (1978) reported similar results from pot culture, suggesting rhizomorph formation may be inhibited in the field by environmental conditions. For other species, observations under artificial conditions do coincide with field behavior (Gregory 1985; Redfern 1975; Rishbeth 1985a,b).

The growth habit of rhizomorphs in soil also varies among species; branching (fig. 4.1) is either monopodial or dichotomous (Morrison 1982b, 1989). This character may have ecological significance since Morrison (1989) found that species with dichotomously branched rhizomorphs tended to be more pathogenic than those producing monopodially branched rhizomorphs, but the distinction was not entirely consistent.

The Effect of Soil on Rhizomorph Growth

Most observations about soil have concerned its influence on the incidence and severity of disease, whereas the primary interest here is effect of soil on the fungus itself. The wide variety of soils associated with disease (Ono 1965, 1970, Rhoads 1956, Ritchie 1932, Shields and Hobbs 1979) suggests *Armillaria* species tolerate a fairly broad range of conditions.

Field observations on effects of soil on disease frequently conflict. Unfortunately, many are of limited value, and may be misleading, because they refer to *A.*

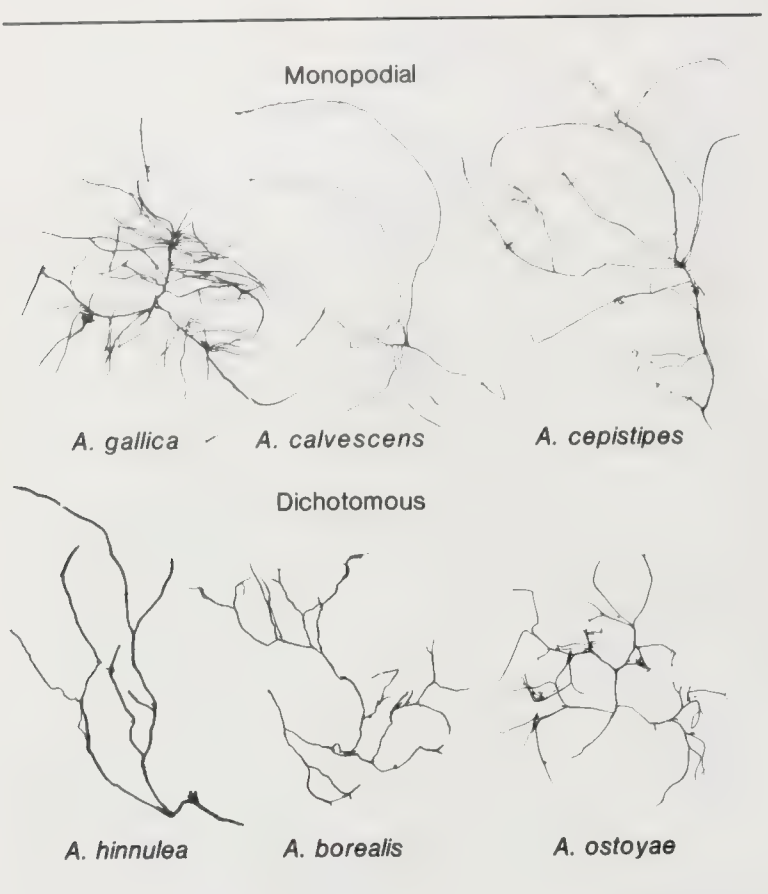


FIGURE 4.1—Variation in rhizomorph growth habit among *Armillaria* species. (Adapted from Morrison 1989).

mellea (*sensu lato*) when more than one species may be present. In these circumstances, differences in disease incidence due to the differing pathogenicity of the species involved may have been incorrectly attributed to soil factors. Similar misinterpretations may also arise through failure to appreciate the effects on disease development of the discontinuous distribution of inoculum.

Experiments in which woody inocula containing *Armillaria* isolates have been allowed to form rhizomorphs in soil (Gramss 1983; Morrison 1976; Redfern 1970, 1973, 1975; Rishbeth 1985b) confirm field observations that *Armillaria* can grow in a wide variety of forest and agricultural soils. Soil seems to exert a major influence on rhizomorph growth only under unusual or extreme circumstances. Thus, pure sand can partially inhibit rhizomorph production (Garrett 1956b, Redfern 1973, Rykowski 1984), whereas peat stimulates growth and branching (Redfern 1973). Certain tropical soils inhibit rhizomorph development (Dade 1927, Fox 1964, Rishbeth 1980, Swift 1968), and the paucity of rhizomorphs associated with damage by *A.*

luteobubalina may also be soil-induced (Pearce and Malajczuk 1990a, Podger and others 1978).

Several methods have been used to assess growth of *Armillaria* from woody inocula in soil. These include measuring the total length or dry weight of

rhizomorphs and repeatedly measuring individual rhizomorphs. Rishbeth (1968) used the last method for testing the effect of temperature, and discussed some problems associated with this type of work.

Moisture

Working with *A. mellea* (*sensu lato*), Garrett (1956b) and Redfern (1970) found soil moisture had no effect on growth within the ranges 40%-80% and 25%-75% of moisture-holding capacity, respectively. Growth of *A. luteobubalina* also occurs over a wide range of matric potentials (-0.0008 MPa to -7 MPa), but it is restricted below -0.6 MPa (which is roughly equivalent to 25% moisture-holding capacity). Seasonal drying may partly explain the paucity of rhizomorphs of this species in Australian soils (Pearce and Malajczuk 1990a). In Britain, Morrison (1976) concluded that seasonal drying may affect growth of *A. mellea* (*sensu lato*) in the upper soil layers.

Waterlogging may restrict growth at depth indirectly through the soil atmosphere (Rishbeth 1978a) and can prevent rhizomorph formation by inocula in pot experiments (Guillaumin and Leprince 1979). Despite the reservations already expressed about field observations, it is notable that *Armillaria* has rarely been reported from permanently wet soils with an appreciable peat accumulation. There is a single observation of *A. ostoyae* from Scotland (senior author and S.C. Gregory pers. comm.), and Hintikka (1974) commented that it seems to be largely absent from forested *Sphagnum* swamps, except where the peat is thin and the ground water is moving.

Temperature

The *in vitro* studies reported in chapter 3 provide a guide to the behavior of the fungus in soil, but caution should be exercised in extrapolating results since important differences may exist. For example, growth occurs at higher temperatures in agar culture than in soil (Rishbeth 1968).

Using woody inocula colonized by a suspension of basidiospores and by measuring growth directly, Rishbeth (1968) found the optimum temperature for rhizomorph growth through soil was about 22°C. Some growth occurred at 5°C and 28°C but none at 30°C. He concluded that rates of spread of about 1.5 m per year observed at sites in southern Britain, where the soil temperature at a depth of 15 cm averages 10°C, roughly corresponded with those determined from his experiments. Later, working with a number of isolates and species, Rishbeth (1978a) found the dry weight of rhizomorphs produced by inocula in soil was usually maximal at 20°C and minimal above 26°C and below

10°C. He suggested the lack of rhizomorph growth in forest soils at low elevations in tropical Africa (Dade 1927, Fox 1964, Swift 1968) may be due to high soil temperatures. By contrast, low temperatures may be limiting in many forest soils, particularly in the north temperate zone during winter (Rishbeth 1978a). However, the production of rhizomorphs from inocula involves two processes: initiation and growth. Initiation may occur over a more restricted temperature range than growth (Rishbeth 1968). Thus, pre-existing rhizomorphs may grow at lower temperatures than indicated by experiments in which rhizomorph production rather than growth is measured. Temperatures below 10°C may therefore be less restrictive than has hitherto been suggested. Although rhizomorph initiation may be curtailed in winter, growth of those initiated at higher summer temperatures may continue.

The effect of low temperatures receives some support from in vitro studies (Hintikka 1974, Pearce and Malajczuk 1990a, Rishbeth 1968), but as indicated earlier, they may not provide an entirely satisfactory guide to behavior in soil and further work is required.

Rishbeth (1978a) found variation in the effect of temperature on rhizomorph growth in soil among a worldwide selection of isolates, but there is little information for different species. Pearce and Malajczuk (1990a) tested growth of *A. luteobubalina* over a limited range of temperatures and found maximum growth at the highest temperature tested (20°C) with virtually no growth at 10°C. On agar, the optimum temperature for growth by this species was in the range 20–26°C, suggesting that it might be somewhat higher in soil. Also on agar, the more northern or high-altitude European species *A. borealis*, *A. cepistipes*, and *A. ostoyae* have a lower optimum for growth than the southern or low-altitude species *A. gallica* and *A. mellea* (Guillaumin and others 1989a). Thus, although there is some evidence for inter-specific variation in the temperature relations of *Armillaria*, further work is required in soil.

Temperature may affect both the number and branching of rhizomorphs initiated from woody inocula. Redfern (1973) found that an isolate of *A. mellea* (*sensu lato*) initiated more rhizomorphs in soil at 25°C than at 15°C, and each system had a greater branching frequency at the higher temperature. This effect requires confirmation and further study with a range of species. The possibility that growth patterns may vary in response to seasonal variations in soil temperature is of particular interest and may have implications for infection and spread.

The studies on *A. luteobubalina* by Pearce and Malajczuk (1990a) demonstrated that rhizomorph behavior may be influenced by an interaction between

temperature and moisture. This may well apply to other species, although the relative importance of the two factors may differ elsewhere.

pH

No body of field observations suggests that pH has a significant effect on *Armillaria*. Gard (1928) associated disease in Persian walnut with a reduction in lime content of the soil, and Rishbeth (1982) recorded killing by *A. ostoyae* on acidic soils but not at comparable sites where soil was alkaline. By contrast, he found *A. mellea* often killed trees on alkaline soils. In an inoculation experiment, Redfern (1978) found that infection by one isolate of *Armillaria* was significantly greater in an acidic soil than in an alkaline soil of similar sandy texture. However, in all these cases any pH effect may have been expressed through the host rather than through the pathogen. Other authors (Kawada and others 1962, Rhoads 1956) refer to killing on acidic soils but this probably only reflects the pH of most forest soils.

Experimental studies of pH effects are hampered by the difficulty of adjusting soil pH. In England, a succession of workers partly avoided the problem by taking advantage of a natural pH variation induced in uniformly sandy soil by differences in the depth of underlying chalk. In an initial experiment, rhizomorph production by a single isolate was greater at pH 7.5 than at pH 4.9 (Redfern 1970). Subsequently, more comprehensive work (Morrison 1974) with a range of isolates gave a variable response, with some isolates being unaffected. Further work by Morrison (pers. comm.) has shown that these differences were related to species. *Armillaria mellea* and *A. ostoyae* grew more in acidic than in alkaline soil, whereas *A. gallica* was either unaffected by pH or favored by alkaline soil. Rishbeth (1985b) tested three species in the same soils but detected no differences.

Inhibitory Substances

After several experiments with sterilized soil extracts, Swift (1968) attributed the absence of rhizomorphs from forest soils in Rhodesia (Zimbabwe) to a water-soluble inhibitor. Olembo (1972) found unsterile leachates of East African soils reduced the colonization of wood by *Armillaria*, but no further work has been done on this topic.

Organic Matter and Soil Nutrient Status

Accumulating evidence suggests soil nutrition affects rhizomorph growth. Rykowski (1984) confirmed the stimulating effect of peat (Redfern 1973) and observed a similar response to pine bark compost. Studying the

influence of various organic soil amendments on rhizomorph development, including peat, Guillaumin and Leprince (1979) obtained rather different results but nevertheless concluded that the surrounding medium affects growth. Morrison (1975) investigated the peat effect and demonstrated that rhizomorph growing tips absorb nutrients. He suggested that the nutrients available from a food base may be supplemented by uptake from soil, and that rhizomorph development may be related to soil nutrient status. Nutrient balance may also be important. Rykowski (1984) found growth in one soil was increased by application of potassium and reduced by nitrogen and phosphorus.

The Distribution of Rhizomorphs in Soil

Soil moisture affects the vertical distribution of rhizomorphs in soil. Morrison (1976) found rhizomorphs grow towards the soil surface, and has suggested this behavior is a response to the oxygen gradient in soil. Vertical distribution is probably controlled by seasonal desiccation of the upper soil layers and by oxygen and carbon dioxide concentrations lower down (Morrison 1976, Rishbeth 1978a). Hartig (1873b) noted rhizomorphs lie at about 10 cm depth, and Lawrence (1910) observed them in "great abundance from 3 to 18 inches below the soil surface." Later authors reported a concentration in the upper soil layers, generally within 10-20 cm of the surface (Day 1927b, Ono 1970, Redfern 1973). Where a humus layer is present, rhizomorphs are more common there than in the mineral soil below (Hintikka 1974, Singh 1981b), an interesting observation in view of the stimulating effect of peat on rhizomorph growth. The concentration of rhizomorphs in the upper soil layers may be important epidemiologically because of the greater vulnerability of trees to infections initiated on the root collar and proximal part of the root system compared to the deeper, more peripheral roots (Bliss 1946, Hintikka 1974, Patton and Riker 1959, Shaw 1980). Inoculum potential may also be greater than with a less stratified distribution.

These field data on rhizomorph distribution are most likely to have been contributed by species which form rhizomorphs capable of extensive growth through soil. Little information is available for species with rhizomorphs which are more closely associated with roots. Pearce and others (1986) found rhizomorphs of *A. luteobubalina* were present on infested sites at depths between 5 and 15 cm. Experimentally, *A. luteobubalina* induced rhizomorphs from woody inocula buried at 10 cm (Pearce and Malajczuk 1990a) although the numerical length were small. For species which infect only by root contact, it seems likely that the infection and spread would be maxi-

mized by an ability to form rhizomorphs throughout the rooting depth of the host.

The horizontal distribution of rhizomorphs can be extensive. *Armillaria gallica* forms a network of rhizomorphs over the surface of living roots (Rishbeth 1985a). Redfern (1973), who probably observed the same species, suggested that rhizomorphs branch and anastomose to form extensive, complex networks which envelop both living trees and the food bases from which they originated. In one new plantation, Redfern (1973) estimated that rhizomorphs had spread up to 35 m in 37 years from adjacent, long-standing woodland infested by *Armillaria*. *Armillaria cepistipes* and other prolific rhizomorph-forming species may behave in the same way. In North America, Lawrence (1910) observed that rhizomorphs growing from infected raspberry canes formed a "network by frequently branching and rebranching", and Childs and Zeller (1929) referred to "a complete network of rhizomorphs about the larger roots" of orchard trees on fir-cleared land infested by a non-pathogenic species. Several authors have estimated the abundance of rhizomorphs in soil (Hintikka 1974; Hood and Sandberg 1989; Ono 1965, 1970; Rykowski 1984). Hintikka recorded 121 cm of rhizomorphs per 100 cm² of soil surface.

Inoculum Potential and Infection

Rhizomorphs represent extensions of inoculum, and are important in the infection, spread, and persistence of many *Armillaria* species. In a minority of species, rhizomorphs are absent or are only sparsely formed, and in these species infection is confined to points of contact between host roots and the inoculum. The infection process may involve epiphytic rhizomorphs or the transfer of mycelium, but the most important feature for the epidemiology of these species is the need for contact between host and inoculum. Infection also occurs in this way under certain environmental conditions which prevent or restrict rhizomorph formation. Garrett (1970) concluded from his experiments with rhizomorph-forming *Armillaria* species that inoculum size, distance between the inoculum and the host, and the influence of environment on the fungus were the major determinants of inoculum potential. However, where infection occurs at root contacts, only the first and last factors seem likely to be important.

This section primarily addresses those factors which affect disease development through their effect on inoculum potential. Chapter 5 describes the infection process in detail; here, attention is confined to the way in which infection occurs and its effect on the epidemiology of disease. The role of wounds in the successful establishment of infection is also considered.

Inoculum Potential

Little work has been done on inoculum potential since Garrett's classical experiments (Garrett 1956b, 1958) and none with species lacking rhizomorphs. Garrett experimented with model systems consisting of small woody inocula and potato tubers in soil. He found rhizomorph growth rate was related to inoculum size, and that the extent of infection in potato tubers increased with inoculum size and decreased with increasing distance between inoculum and tuber. Rhizomorph growth rate also declined with time, and he attributed this partly to nutrient depletion in the inoculum and partly to competition for nutrients between the main apex of a rhizomorph system and its subordinate branch apices. Rykowski (1984) recently confirmed Garrett's results, using larger inocula and Scots pine seedlings. He used indices derived from the number, length, and weight of rhizomorph systems produced from inocula, and the number of apices on those systems, to calculate the "potential infection threat" presented by inocula in various soils.

Although the concept of inoculum potential is simple and of considerable biological importance, it is difficult to envisage its application to individual trees since field situations are frequently complex. Inocula are rarely discrete, and infection often is not readily associated with specific point sources. Also, inocula vary in size from parts of individual roots to entire stumps.

The rhizomorph networks formed by some species may present an additional complication. The behavior of these systems requires study. Redfern (1973) suggested they may be relatively long-lived, being supported by a succession of food bases as they become available to different parts of the network, and the direction of nutrient flows changing to maintain the entire system from different sources. This is apparently inconsistent with experiments on translocation (Anderson and Ullrich 1982b, Schütte 1956) which have shown that it only occurs towards growing tips. Morrison (1975) found that nutrients absorbed by growing tips were not translocated towards the food base. These experiments do not represent the behavior of an entire network, however, and they are not inconsistent with the possibility that the direction of translocation within a rhizomorph in a network may vary with time. Anderson and Ullrich (1982b) commented that "if the (rhizomorph) base were converted to a sink for nutrients, as may be the case during fruiting or exhaustion of food reserves, rhizomorphs may transport nutrients from tip to base." This is supported by observations on severed rhizomorphs. Rhizomorphs forming part of a network and which are severed in situ initiate new rhizomorphs simultaneously from the cut ends, as do

excised sections of large diameter rhizomorphs (Hintikka 1974, Redfern 1973, Rykowski 1984).

The principle of a fungal *corpus* consisting of a network of colonized stumps and rhizomorphs may apply equally well to species such as *A. mellea*, *A. ostoyae*, and *A. hinnulea* with more restricted rhizomorph-forming abilities. Roots may simply predominate over rhizomorphs in the network. However, some evidence indicates that, in contrast to *A. gallica* and *A. cepistipes*, rhizomorphs of *A. mellea* are short-lived and are produced in successive waves (Guillaumin and others 1989a) which suggest these species are unlikely to form persistent networks.

Clearly, much of the foregoing is speculative, but it is worth consideration since rhizomorph systems which behave in this way might create inocula consisting effectively of several stumps.

Despite this complexity, and notwithstanding the minute inocula used by Garrett (1956b) and Rykowski (1984) compared to substrates available naturally, there seems no reason to doubt the general applicability of the principle of inoculum potential to such large inocula. Inoculum potential is maximized where healthy roots and inoculum are in contact; where gaps are bridged by rhizomorphs, it diminishes with increasing distance between them. However, few detailed analyses of disease patterns in relation to the distribution of inoculum have been done. Understanding such patterns requires considerable knowledge of pathogen behavior in the circumstances of each outbreak, particularly the relative importance of rhizomorphs and root contacts as the means of spread in the species involved.

Shaw (1980) and Shaw and others (1976a) described a relatively straightforward situation in young ponderosa pine involving a single species, *A. ostoyae* (Shaw 1984), spreading essentially by root contact from discrete sources of inoculum. On the other hand, disease development following replacement of indigenous forest comprising many host species and more than one *Armillaria* species by a susceptible monoculture (MacKenzie and Shaw 1977) is much more complex. Under these circumstances, the pattern of mortality assessed on a single occasion (van der Pas 1981a) may be difficult to interpret (Roth and others 1979). MacKenzie and Shaw (1977) recorded decreasing mortality with increasing distance from infected stumps. Though such a pattern suggests the stumps were acting as the initial infection sources, interpretation of subsequent events in terms of inoculum potential is not possible. As suggested by Roth and others (1979), the effect could be caused by rapid, early killing within the rooting zone

of the stumps acting as inocula, followed by a slower rate of mortality outside this zone as growing roots or rhizomorphs bridge the gaps between potential hosts and inocula.

In another example, similar patterns of mortality among saplings around eucalypt stumps infected by *A. luteobubalina* (Pearce and others 1986) may simply have reflected the time when the developing sapling root systems made contact with stump roots. Alternatively, disease centers in young conifers (probably caused by *A. ostoyae*) show reduced extension rates because of increasing host resistance (Redfern 1978) rather than declining inoculum potential with increasing distance from a point source.

On a large scale, the effect of an increase in inoculum can be appreciated readily. Forestry operations such as clear-felling, selective cutting, thinning, the treatment of indigenous crops with herbicides, or events such as fire provide opportunities for a massive increase in inoculum (Kile 1980b, Pronos and Patton 1978, Rishbeth 1972b, Shaw and others 1976a, Swift 1972, van der Pas 1981b). For pathogenic species, more inoculum typically results in more disease. Thus, *A. luteobubalina* causes disease in unlogged eucalypt forest (Kile 1983b), but the greatest incidence and severity of disease is associated with logging (Kellas and others 1987, Pearce and others 1986). Concomitantly, natural regeneration or planting repositions hosts relative to the inoculum. Thus, in former disease centers which are devoid of hosts, or in plantation systems where trees are planted beside stumps which may subsequently become colonized, the distance between potential hosts and inoculum may be small.

Physical disturbance of the soil by logging, plowing, scarifying, or even planting may sever rhizomorph networks, which respond by initiating new growing tips from the cut ends. Besides increasing the amount of inoculum and perhaps the availability of new and more susceptible hosts, harvesting disturbance can also stimulate the production of rhizomorph growing tips and locally increase the chance of infection (Redfern 1973, Rykowski 1984, see chapter 11).

Inorganic fertilizers may influence inoculum potential through the soil environment. The effect of some macro-nutrients on rhizomorph production by inocula in soil has already been mentioned (Rykowski 1984). The inoculum may also be directly affected. Work by Connolly (1970-71), Garrett (1953, 1970), and Rykowski (1984) suggests the possibility that crop fertilization may increase inoculum potential by changing substrate quality when roots with an enhanced nutrient status eventually become inoculum. Both of these interesting possibilities merit further study.

To assess the need for control in *Armillaria*-infested areas (see chapter 11), forest managers must estimate the inoculum potential of the species present in addition to knowing their pathogenicity and distribution. However, even in the simplest situation involving only one species, there seems little possibility that the inoculum potential of *Armillaria* on a site could be assessed by casual observation. For example, although it has been used for modeling purposes (see chapter 10), stump size may be a poor guide unless colonization is complete. The circumstances under which complete colonization may be achieved include the invasion of living, susceptible conifers by highly pathogenic species, the colonization of freshly felled conifers by growth of the same species from root lesions, and the colonization of healthy conifer stumps by species capable of forming extensive rhizomorph systems. In hardwoods, however, colonization may be restricted in those species which tend to regrow after cutting (Rishbeth 1972b). In some eucalypts (Kile 1980b), and possibly oaks, the heartwood is resistant to decay and remains uncolonized. Pearce and others (1986) found a significant relationship for *A. luteobubalina* between an estimate of how much inoculum was provided by individual, infected stumps and mortality in nearby saplings; assessments like this are unlikely to be feasible in commercial forestry, however.

A reduction in inoculum potential or the prevention of inoculum buildup provides the basis for many control measures (see chapter 11). Under natural conditions, the amount of *Armillaria* inoculum on a site may be reduced by competition from other fungi and by fire. In the case of wood-rotting fungi which are also parasites, such as *Phellinus weirii* (Morrison and others 1988) and *Heterobasidion annosum* (Greig 1962), competition is not beneficial; but some saprophytic decay fungi are also able to compete successfully and may be useful for biological control (Pearce and Malajczuk 1990b, Rishbeth 1976). The soil-inhabiting fungus *Trichoderma viride* may exert a degree of control which can be enhanced by soil fumigation (Bliss 1951; Garrett 1957, 1958; Ohr and others 1973). Fire may kill rhizomorphs in soil (Hood and Sandberg 1989), but its effects on inoculum survival and subsequent rhizomorph activity are unknown.

A massive inoculum is not a prerequisite for infection if the distance between inoculum and host is minimal. Many experiments have demonstrated that successful infections can be established on small trees by means of small woody inocula, some weighing as little as a few grams (Patton and Riker 1959, Rykowski 1984). This has particular relevance for control by inoculum removal since root fragments inevitably remain after destumping and root raking operations (Morrison and others 1988). Although a high level of control can be

achieved by destumping, certainly a level which would return an infested site to normal productivity, residual root fragments may nevertheless permit the re-establishment of disease. Damage may be confined to a few early losses, but it could be extended by secondary, tree-to-tree spread (Rykowski 1984).

Although small and large inocula may both cause infection, Rykowski (1984) has suggested that each represents a different type of threat. In experiments with small, woody inocula, rhizomorph production per unit volume of inoculum was inversely related to total inoculum volume. This suggests that rhizomorph production is delayed until the substrate has been fully colonized and certain nutritional requirements have been met (Benjamin and Newhook 1984b, Garrett 1953, Patton and Riker 1959, Rykowski 1984). Rykowski concluded that whereas in small substrates the phases of colonization, rhizomorph production, and exhaustion are accomplished rapidly, the same process takes longer in larger inocula. He argued that stumps may behave in the same way, presenting short-term and long-term infection threats, respectively.

Infection

As already discussed, rhizomorphs are formed in soil to a greater or lesser extent by most *Armillaria* species; the absence of rhizomorphs is apparently uncommon among species in the genus. In some species, they are restricted to root surfaces or to the close proximity of roots, whereas others form abundant rhizomorphs which ramify freely through soil. Without rhizomorphs, infection is confined to points of contact between host roots and the inoculum; with increasing rhizomorph production, infection can also take place at greater distances from the inoculum.

Because rhizomorphs are often abundant, much of the early literature from temperate countries emphasized the importance of rhizomorphs growing freely through soil as a means of spread. Indeed, some authors considered them essential (van Vloten 1936). However, a number of authors either observed infection at root contacts (Kawada and others 1962, Přihoda 1957, Zeller 1926) or inferred its occurrence from their observations (Marsh 1952, Molin and Rennerfelt 1959). Working in black currant plantations, Marsh (1952) found the pattern of disease spread was best explained by root contact infection rather than by rhizomorphs growing in soil unoccupied by roots. Molin and Rennerfelt (1959) concluded that spread occurs mainly by root contact, and rhizomorphs only play a secondary role except over distances less than 1 m. In Czechoslovakia, Přihoda (1957) referred specifically to infection of Norway spruce both by rhizomorphs and by the transfer of mycelium at root contacts where rhizomorphs were ab-

sent. He commented that although soil rhizomorphs were present on one site, they were sparse and weak and the bulk of infection was by mycelium transfer. He discussed the possibility that rhizomorph formation might be inhibited by alkaline soils, but he concluded that soil was unimportant and that some "forms" of *Armillaria* do not produce rhizomorphs whereas others do so abundantly.

Without our present understanding of *Armillaria* speciation and ecology, earlier authors did not appreciate the difference between spread of the more pathogenic species among susceptible hosts and the spread of less pathogenic species on stumps and weakened trees. Přihoda's comments (1957) were therefore particularly pertinent. These European observations of spread by root contact probably referred to either *A. ostoyae* or *A. mellea*, which are pathogenic and form fewer rhizomorphs than the weakly pathogenic species *A. gallica* and *A. cepistipes* (Guillaumin and others 1985, 1989a; Rishbeth 1985a). Abundant rhizomorph production by the latter species may also prompt misinterpretation where they occur with pathogenic species if it is assumed that any rhizomorphs observed in soil are those of the disease-causing species.

For species such as *A. tabescens*, *A. hinnulea*, and *A. luteobubalina* in which rhizomorphs are either absent or confined to root surfaces, infected roots must be in contact with potential hosts, or very close to them, for infection to occur (Kile 1980b, 1981; Kile and Watling 1983; Pearce and others 1986; Shearer and Tippet 1988). Nevertheless, interlocking root systems can provide highly effective pathways for spread by pathogenic species among susceptible hosts. Surveying dieback in messmate stringybark and mountain ash associated with *A. hinnulea* (Kile 1980b, Kile and Watling 1983), Kile (1980b) found that 74% of living trees had infections or epiphytic rhizomorphs on the root system. By contrast, species which form extensive rhizomorph systems, such as *A. gallica* and *A. cepistipes*, are not restricted in this way. *Armillaria mellea* and *A. ostoyae* have a lesser ability to form rhizomorphs in soil than *A. gallica*, but they are not confined to root surfaces and these species may occupy an intermediate position. In ponderosa pines, *A. ostoyae* spread between roots near to each other as well as at contacts (Shaw 1980).

In New Zealand, free-growing rhizomorphs are common in soil where both *A. limonea* and *A. novae-zelandiae* are present (Hood and Sandberg 1987), but the relative contribution of each species to the rhizomorph population is unknown. However, both species readily produce rhizomorphs in pot culture (Benjamin and Newhook 1984b), so it is likely that rhizomorph spread is important in both cases.

Recent work has suggested a relationship between rhizomorph production and pathogenicity among some European species. The more pathogenic species tend to produce smaller rhizomorph systems than less pathogenic species (Gregory 1985; Guillaumin and others 1985, 1989a; Redfern 1975; Rishbeth 1985a). Some evidence indicates the relationship may also apply to North American and Australasian species (Morrison 1989). Further information, particularly about rhizomorph production, is required for many of the more recently described species, but differences appear to be large (Gregory 1985, Redfern 1975) and may have considerable ecological significance. For a weak pathogen, a strategy involving a wide dispersion of inoculum offers the advantage of position when potential food bases become available. Thus, weakly pathogenic species which form extensive rhizomorph systems and infest roots in a network of rhizomorphs are able to exploit this advantage in the acquisition of substrates, which may consist of stumps or living trees with declining resistance. More pathogenic species, by contrast, do not require such a strategy and are able to spread among susceptible hosts through root contacts.

It follows from this discussion that spread in pathogenic species is likely to be influenced more by factors affecting the distribution of tree roots than by those which affect rhizomorph development. Thus, for purposes of disease management, pathogenic species in North America and Europe should perhaps be considered to have a greater affinity with *Phellinus weirii* or even *Heterobasidion annosum* than they traditionally have been.

Before our present understanding of speciation and pathogenicity in the genus, considerable debate focused on the environmental conditions required for infection and on the need for infection courts provided by root wounds or debilitated roots. The distinction is important since otherwise healthy roots which are physically wounded, perhaps by abrasion against stones, by animals, or by harvesting machinery, differ greatly from roots debilitated by, for example, poor soil aeration.

From the many inoculations which have been done on wounded roots, little doubt remains that infection can take place through wounds; but their importance as natural infection courts, however, has not been established clearly. Dimitri (1969) concluded that although infection in Norway spruce can take place through undamaged roots, it occurs primarily through wounds and dead roots. Buckland (1953) reported that it was difficult to detect infection through healthy bark of Douglas-fir, observing it only in roots which were mechanically damaged or physiologically debilitated. Antikka (1974) believed root collar in-

juries caused by snow bend promoted rhizomorph penetration at this point. However, it is difficult to determine by observation alone the role of wounded or stressed roots in the establishment of infection. In one of the few inoculation experiments designed to test the effect of wounding, Weaver (1974) found that it increased the number of isolates of *A. tabescens* which were able to infect peach roots. Invasion was also more extensive in injured roots. More recently, Whitney and others (1989b) found wounding increased infection in balsam fir inoculated with *A. ostoyae*.

Evidence from natural disease outbreaks, and the ease with which unwounded trees can be infected in inoculation experiments, suggest that, at least for the more pathogenic species, wounds are unlikely to increase the success of infection. Wounds and debilitated roots could be important infection courts for less pathogenic species such as *A. gallica*, but no evidence supports this. Gregory (1985) showed that the length over which rhizomorphs became attached to the host surface was greater for species of low pathogenicity than for those of high pathogenicity. This could be expected to provide weakly pathogenic species with a greater opportunity to encounter wounds than would be available to pathogenic species.

Conclusions

Wood, mainly tree roots, provides the major source of inoculum for *Armillaria*. Many older observations of disease supported the view that hardwoods provide a superior substrate for *Armillaria* than conifers. In general, little experimental evidence substantiates an intrinsic difference between the two substrates but stumps of broadleaved trees may exhibit greater longevity as inoculum. Some *Armillaria* species may subsist better on particular food base species, but there is no evidence for substrate specialization. However, a degree of ecological specialization is known for some north-temperate species.

All species form rhizomorphs in culture, and almost all do so in forest soils, but they vary greatly in the amount of rhizomorph growth. Some species are epiphytic or restricted to the close proximity of roots, whereas others grow freely through soil, forming networks which link both colonized stumps and living trees. Infection is probably caused by rhizomorphs in most species, either at contacts between host roots and the inoculum or at some distance from the inoculum. For species lacking rhizomorphs, or where soil conditions prevent their formation, infection is restricted to contacts and occurs by the transfer of mycelium. Species with epiphytic rhizomorphs are similarly restricted, but infection can be either by mycelium transfer or by rhizomorphs. The relative importance of

the two methods for these species is unknown. No information is available about the influence of soil on infection by mycelium transfer.

The environment can have a major effect on *Armillaria* through the effects of competing fungi on survival in woody substrates and through the influence of soil on rhizomorph growth. The fungus can grow in soils derived from a wide variety of lithologies, but more fertile soils may be particularly favorable since nutrient uptake from the soil may supplement nutrients from the food base. Soil moisture, temperature, and pH all affect rhizomorph growth, and there is some evidence for an interaction between moisture and temperature which may also be important. Species differ in their response to temperature and pH, but little information is available.

The inoculum potential of *Armillaria* is influenced by the amount of inoculum, by the distance between the inoculum and the host, and by environmental effects. Forestry operations such as felling and thinning increase inoculum on a site, but patterns of mortality should not be interpreted simply in terms of inoculum

potential. Interaction between, among other things, the amount and distribution of inoculum, the method of spread by the *Armillaria* species involved, and root system development by the host may be equally important.

The more pathogenic *Armillaria* species may produce smaller rhizomorph systems than less pathogenic species. Further information is required, particularly for more recently described species, but such a tendency may have considerable ecological significance. Thus, the extensive rhizomorph systems produced by weakly pathogenic species may represent a strategy for the wide dispersal of inoculum in order to gain the advantage of position when potential substrates become available. By contrast, the interlocking root systems of susceptible hosts may provide an effective means of spread for more pathogenic species, and obviate the need for extensive rhizomorph systems.

Wounds may be important infection courts for weakly pathogenic species, but they are unlikely to increase the success of infection by more pathogenic species.

Infection, Disease Development, Diagnosis, and Detection

Duncan J. Morrison, Ralph E. Williams, and Roy D. Whitney

The first comprehensive description of Armillaria root disease, including the causal fungus and its life cycle, was made by Robert Hartig (1874). He recognized that *Rhizomorpha fragilis* Roth with its two chief forms, *R. subterranea* and *R. subcorticalis*, composed part of the mycelial body of *Agaricus (Armillaria) melleus*. *Rhizomorpha subterranea* and *R. subcorticalis* were the binomials applied to the cylindrical brown to black mycelial strands found in soil and on root surfaces and the flattened white to cream colored mycelial felts (fans) found between the bark and wood of hosts, respectively. Hartig observed the basidiomes of *A. melleus* developing on rootstocks with *R. subcorticalis* under the bark and on rhizomorph apices in soil. He also described infection and disease development in several conifer species.

Since Hartig's work, more than 600 species of woody plants have been recorded as hosts of *Armillaria* species (Raabe 1962a). The infection process and disease development have been described for several hardwood and coniferous hosts. A wide variety of symptoms, signs, and host responses resulting from disease have been recorded, reflecting the wide host and geographical ranges and number of *Armillaria* species. This chapter describes the infection process and disease development in photosynthesizing (green) plants, the symptoms and signs on diseased plants, and how these symptoms can be used to detect Armillaria root disease in forests and orchards.

The Infection Process and Disease Development

The Infection Process

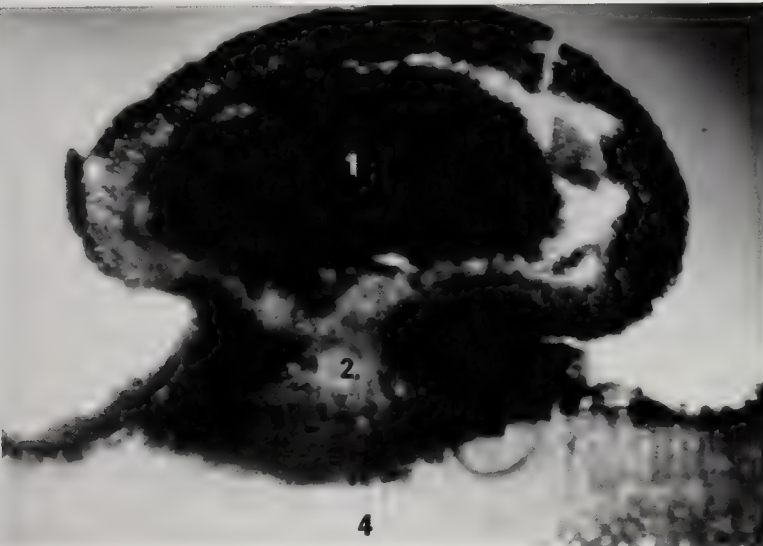
Thomas (1934) defined infection by Armillaria root disease as the penetration of the fungus into the host, with or without subsequent colonization. The roots of woody plants are infected following contact between a rhizomorph or diseased root. Al-

though many records document many different hosts being attacked (Raabe 1962a), the literature on the infection process is sparse. All detailed studies of the infection process predate acceptance by pathologists that *Armillaria mellea sensu lato* represents many species. Diverse host responses and sometimes conflicting reports about the same host are evident in accounts of disease occurrence. These apparent discrepancies may be partly attributable to different *Armillaria* species having been involved. Current knowledge of the geographical distribution and host preferences of *Armillaria* species helps clarify the identity of *Armillaria* species reported in early studies. For example, the *Armillaria* on pine (Hartig 1874) is probably *A. ostoyae* (H. Marxmüller pers. comm.) and Thomas' (1934) studies on hardwood trees probably involved *A. mellea sensu stricta*.

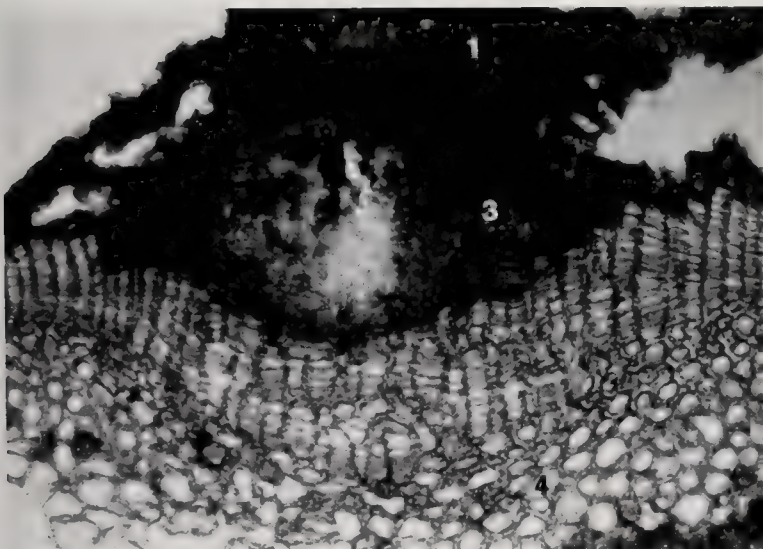
The first account of the *Armillaria* infection process was given by Hartig (1874). He wrote, "The killing of roots is brought about by *Rhizomorpha fragilis* which bores into the root, spreads out in all directions as *R. subcorticalis* and thus from the point of attack continually approaches the root stock until this is reached."

General agreement exists among the detailed studies of coniferous (Day 1927b, Rykowski 1975, Woeste 1956) and hardwood hosts (Guillaumin and Rykowski 1980, Thomas 1934) about the infection process by rhizomorphs. A rhizomorph becomes attached to a root initially by hardening of the mucilaginous substance which covers its growing tip. Then, single hyphae developing from the rhizomorph tip and penetrating the outer layer of cork cells anchor the rhizomorph to the root. On susceptibles with smooth bark, branches which will form the root-penetrating rhizomorph develop at points of firm contact with the root surface. The branches originate in the inner cortical cells of the rhizomorph when hyphae divide and spread laterally. These hyphae force their way through the outer cortical cells of the rhizomorph and emerge as a branch. Branches may be numerous and always develop on the side of the rhizomorph contacting the host (Thomas 1934).

Thomas (1934) studied how *Armillaria* infected fleshy and woody roots of susceptible and resistant hosts. Penetration of the rhizomorph was essentially the same for both groups. The lateral branch, acting as a unit, not as individual hyphae, begins to penetrate by mechanical force. The host cork cells under the rhizomorph are pushed in and slightly compressed (figs. 5.1A,B). At this stage, tissues below the cork cells appear disorganized, which is attributed to secretions from the rhizomorph. Penetration continues by a combination of chemical and mechanical means. Beneath the cork, the rhizomorph branches spread laterally and radially into bark tissues. The descriptions of this process by Day (1927b) and Woeste (1956) indicate that more chemical destruction of tissues occurs in conifers than in hardwoods. Enzymatic breakdown of suberin may also be involved in bark penetration (Swift 1965, Zimmermann and Seemüller 1984).



A



B

FIGURE 5.1 — Penetration of the bark of a walnut root by *Armillaria mellea*. A: Subterranean rhizomorph with a developing lateral branch; B: Infection wedge penetrating host bark (1- rhizomorph; 2- rhizomorph branch; 3- infection wedge; 4- host bark). (J.J. Guillaumin)

In susceptibles with scaly bark, the rhizomorphs (*R. subterranea*) run tangentially under bark scales becoming *R. fragilis* (Woeste 1956); that is, white strands without a rind. Rhizomorphs may emerge successively from beneath bark scales along a root. *Rhizomorpha fragilis* (as *R. subcorticalis*) may penetrate the bark scales and develop infection wedges beneath each one. Cell walls turn brown and cell contents become disorganized some distance from the infection wedge.

Day (1927b), Thomas (1934), and Woeste (1956) concluded that rhizomorphs of *Armillaria* need neither wounds nor anatomical points of weakness to attack healthy, vigorously growing susceptibles. However, root injuries caused by stones and wind-induced root movements, wounds made by insects and scarification equipment, and rootlets killed by excessive moisture could all serve as infection courts (Basham 1988, Dimitri 1969, Kile 1981, Rizzo and Harrington 1988b, Whitney 1961). Two years after inoculation with *A. tabescens*, most isolates had infected injured roots of peach, whereas only a few isolates had infected uninjured ones, and invasion of injured roots was usually more extensive (Weaver 1974).

Zeller (1926) described infection of susceptible roots by mycelial transfer across points of contact with diseased apple roots. He suggested that infection of the susceptible root begins when its healthy bark is acted upon by toxic substances produced by *Armillaria* in the contacting diseased root. Shallow brown spots appear in the bark's outer parenchyma, and these eventually coalesce. Flakes of dead cork are sloughed as new cork layers are formed. *Armillaria* mycelium was not found in the spots until two or more plates of cork had been sloughed. Eventually, the fungus reaches the cambium and a canker develops. Conifers may become infected in a similar manner (Morrison unpubl.). Initially, mycelial fans of *A. ostoyae* grow in a root's outer bark. As the area of colonized bark increases, mycelial fans penetrate to the cambium. Bark tissue becomes necrotic in advance of the mycelial fans.

Host Response to Infection

Host responses to *Armillaria* root disease fall into three categories: exudate production, meristematic activity, and biochemical interaction. At the biochemical level, fungal infection involves an interaction between compounds already present in the host or induced by infection and extracellular fungal metabolites. These biochemical interactions are discussed in chapter 3. Here, responses involving meristematic activity and exudates are discussed.

Meristematic activity leading to cork and callus formation and, frequently, adventitious roots is a common

host response to *Armillaria* infection on roots and at the root collar. Most descriptions of the infection process by rhizomorphs indicate that all living, vigorous suspects responded to bark penetration by forming one or more secondary cork layers beneath the point of penetration. Thomas (1934) noted that in resistant hosts the lesion produced by initial penetration was walled off by the secondary periderm; this cork layer then widened with root growth. In susceptible hosts, penetrating rhizomorphs breach these secondary cork layers. Rykowski (1975) observed similar reactions in Scots pine roots. On some roots, the penetrating rhizomorph reached the cambium whereas on others secondary cork isolated the infecting mycelium from living host tissues and caused infected bark to be sloughed (fig. 5.2). Observations on plum rootstocks showed that their resistance to *A. mellea* was mainly due to post-infection reactions, because the success rate in penetration by the fungus was similar for susceptible and resistant rootstocks (Guillaumin and others 1989b). Mycelial fans in the bark and sapwood grew considerably less in resistant rootstocks, and the slower growth was associated with pink or purple discoloration of bark and wood tissues surrounding lesions (fig. 5.3).

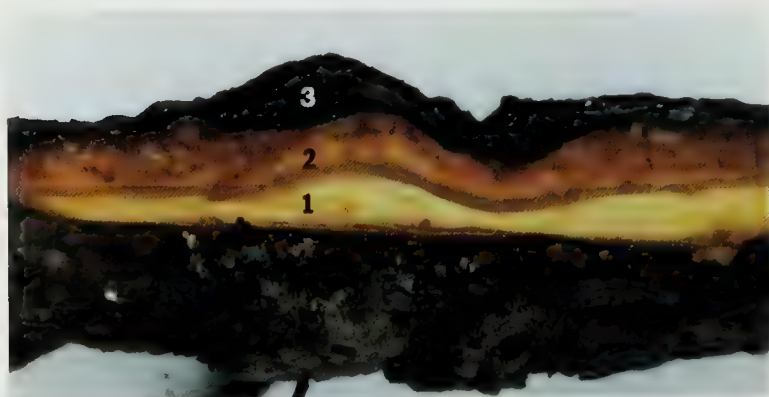
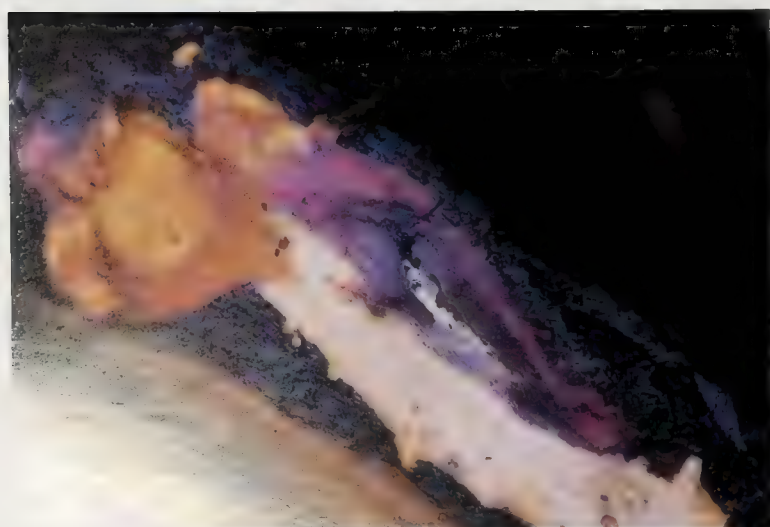


FIGURE 5.2 — *Armillaria ostoyae* lesion on a Douglas-fir root in which secondary bark has isolated the infecting mycelium (1-xylem; 2-bark; 3-infected bark). (D.J. Morrison)



Armillaria mellea lesion on a resistant *Prunus* sp. showing discoloration of bark around the lesion.

Perhaps this post-infection reaction, which only occurs in living tissues, kills the mycelium thus preventing disease development.

Many hosts respond to *Armillaria* attack by exuding resin, gum, or kino. In hardwood hosts in which a pathogenic *Armillaria* species had penetrated to the cambium, Thomas (1934) observed that the xylem became brown ahead of penetrating hyphae. This reaction appeared to result from a gummy deposit in the vessels, perhaps secreted from the affected cells or a product from their walls. Resin production in pines was confined to areas of bark where mycelium had penetrated to the cambium and was not associated with ectotrophic spread in bark scales (Redfern 1978). On 5-year-old Corsican pine, the resin response was much more vigorous on trees inoculated with *A. mellea* than with *A. ostoyae* (Rishbeth 1982). Copious resin formed beneath bark tissue infected by *A. mellea*, forcing the tissue away from the root wood. Some mycelial sheets of *A. mellea* containing the resin were not viable, while those of *A. ostoyae* appeared to be unaffected (Rishbeth 1982).

The effects of conifer resin or resin components on *Armillaria* growth in culture vary. Pinene inhibited growth of *A. ostoyae* and *A. gallica* (Entry and Cromack 1989) and volatiles in Scots pine oleoresin reduced the growth of *Armillaria* by one-half (Rishbeth 1972a). However, powdered wound resin from ponderosa pine, when added to malt extract agar, significantly increased *Armillaria* growth compared to the basic medium (Shaw and Roth 1976).

Similarities may exist between *Heterobasidion annosum* (Fr.) Bref. and *Armillaria* in how oleoresin affects mycelial growth. Oleoresin did not affect *H. annosum* growth in agar culture. Prior (1976) suggested that resin-impregnated root wood of Corsican pine was a physical impediment to the fungus, reducing mycelial growth rate by more than one-half compared to non-resinous roots. Rykowski (1975) observed that resin-soaked wood and callus around root lesions on Scots pine limited spread of *Armillaria*; hyphae were not found in the resinous wood. Similarly, in roots of young, vigorously growing Douglas-fir trees, the host checked infections by laying down a callus and resin barrier (Buckland 1953), thus forming a latent canker (fig. 5.4). Cankers were 2-3 cm long, covered with resin, bounded by callus tissue, and often several years old. Within cankers, *A. ostoyae* either remained dormant or grew into the woody core of the root. Lesions at the root collar developed from one or more diseased lateral roots (Day 1927b). After killing the cambium at the root collar and on the lower bole, further spread of *Armillaria* was checked and callusing occurred (figs. 5.5A,B). In conifer roots, a central column of decay caused by *Armillaria*



FIGURE 5.4 — *Armillaria ostoyae* lesion on a Douglas-fir root. Note callusing at the margin of the lesion. (G.W. Wallis)

was compartmentalized by a barrier zone consisting of complete rings of resin ducts and parenchyma or numerous resin ducts separated by tracheids (Tippett and Shigo 1981).

In eucalypts, the development of decay in the roots and lower bole reflects differences in their response to *A. luteobubalina* (Shearer and Tippett 1988). Roots of jarrah often had bark lesions which were confined by new layers of periderm. Barrier zones formed in the xylem as a result of infection and were obvious boundaries between xylem produced before and after infection (fig. 5.6). *Armillaria luteobubalina* often girdles wandoo at the root collar because the tree does not resist tangential spread of the fungus in the inner bark. In contrast, callus tissue formed by jarrah and messmate stringybark restricted tangential spread, causing inverted V-shaped lesions (Kile 1981, Shearer and Tippett 1988). On citrus trees attacked by *A. tabescens*, living roots had bark lesions up to 30 cm long, some of which were delimited by callus (Rhoads 1948).

Adventitious roots arising from callus tissue (fig. 5.7) may compensate for roots killed by *Armillaria* root disease (Cooley 1943, Kile 1980b, Riggensbach 1966, Rishbeth 1985b).

The incidence of mortality by *Armillaria* root disease often decreases with increasing plant age, particularly in conifers (Buckland 1953, Gibson 1960, Johnson and others 1972, MacKenzie 1987). This decrease usually is attributed to increased host resistance with age, which could be associated with physiological or biochemical changes in the host. In lodgepole pine, resin production increases with age until about 50 years (Shrimpton 1973). The ability of conifers to form callus where lesions form on lateral roots and the root collar increases between age 5 and 20 years (Johnson and others 1972).

Post-Infection Development

Post-infection development of *Armillaria* root disease in a host root system depends upon the susceptibility, size, and age of the host (see below), the pathogenicity (see chapter 6) and inoculum potential (see chapter 4)



A



B

FIGURE 5.5 — A: *Armillaria ostoyae* lesion on the lower bole of a 21-year-old Douglas-fir. Note loosened bark and blackened resin. B: Cross section through lesion in (A). Note active callusing of lesion. (D.J. Morrison)



FIGURE 5.6 — *Armillaria luteobubalina* lesion on a greatcone banksia root. One side of the root was killed by the fungus. The area of xylem discoloration is bounded by a barrier zone. (Figure 5E from Shearer and Tippet 1988)



FIGURE 5.7 — Adventitious roots arising from a callused *A. ostoyae* lesion on a Douglas-fir root (1- living root; 2- adventitious roots; 3- *A. ostoyae*-killed root). (D.J. Morrison)

of the fungus, and the influence of environment on host-fungus interaction (see chapters 7, 8). In susceptible hosts, the rhizomorph which causes infection penetrates to the cambium, becomes *R. subcorticalis*, and spreads laterally in all directions through the cambial zone (Woeste 1956). Growth of mycelial fans in the outer bark may precede that in the cambium; that is, growth is ectotrophic. The extent of ectotrophic growth is variable. In messmate stringybark mycelium of *A. luteobubalina* in the outer bark was up to 1 m ahead of cambium infection (Marks and others 1976). In Scots pine (Redfern 1978), mycelium of *A. ostoyae* was only 2 cm ahead of established infection proximal to the infection point. As occurs with the penetrating rhizomorph branch, mycelial fans act as a unit, and host tissues are affected ahead of them. Schmid (1954) described the invasion of spruce bark by *R. subcorticalis*. In the xylem,

mycelium penetrates the rays and spreads from them laterally into the xylem elements (Dade 1927, Woeste 1956). Continued killing of host tissues in the cambial zone girdles the root. The fungus spreads distally and proximally from the point of infection, and on reaching the root collar it spreads to other primary roots.

The location of infections is an important factor in disease development. Whether the result of contact with rhizomorphs or diseased roots, infections at the root collar or on the tap root (if present) usually kill the host more rapidly than infections on lateral roots (Barss 1913, Gadd 1930, Shaw 1980). However, infections at either location may be lethal (Rhoads 1948). On sapling and pole-sized ponderosa pines, Shaw (1980) found that rhizomorph-initiated infections on lateral roots were common, although the fungus rarely advanced proximally more than a short distance from a girdling root lesion. *Armillaria* infections on lateral roots may have failed to spread proximally because of host response, because rhizomorphs and distal portions of small roots may have provided inadequate inoculum potential, or both. Lethal attacks occurred high on the tap root or on the root collar. Similar observations were made on young Douglas-fir (Buckland 1953), on red pines and eastern white pines, and on white spruce (Patton and Riker 1959). Rykowski (1975) described the development of disease in the root systems of Scots pines, showing seven distinct patterns of infection.

Where rhizomorphs cannot establish progressive infections or for species which do not form them in forest soils, infections develop at contacts between healthy and diseased roots. Contacts are more likely to occur on lateral roots than at the root collar. On cacao (Dade 1927), citrus (Rhoads 1948), Douglas-fir (Morrison 1981), and eucalypts (Pearce and others 1986, Podger and others 1978, Shearer and Tippet 1988), infections originating this way on lateral roots spread to the root collar (fig. 5.8) and then to the tap root and other lateral roots, eventually girdling the trunk.

When *Armillaria* girdles a root, the portion distal to the infection is colonized rapidly by mycelial fans growing in the cambium (Redfern 1978, Shaw 1980). Redfern (1978) observed maximum spread of 110 cm (mean 62 cm) in 10 months in inoculated roots which had been severed.

Effects on the Host

In agricultural crops, *Armillaria* root disease may reduce the quantity and quality of produce prior to a plant's death. In forest crops, the disease may reduce height and diameter growth, cause decay of the bole, or cause death of the host, directly or indirectly.

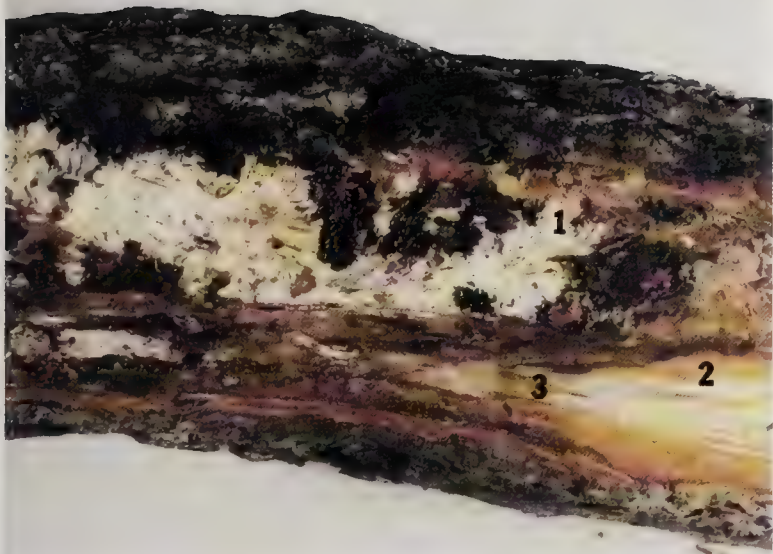


FIGURE 5.8 — *Armillaria ostoyae* infection spreading along a Douglas-fir root (1- mycelial fan in outer bark; 2- bark necrosis in advance of the mycelial fan; 3- cambial necrosis). (D.J. Morrison)

Reduction in height and diameter increment is a consequence of partial killing of the host's root system. Ten-year-old radiata pine showed a highly significant difference in cumulative mean increment between healthy trees and those with more than 65% of root collar circumference showing symptoms of *A. limonea* or *A. novae-zelandiae* (Shaw and Toes 1977). Diameter growth of 70- to 80-year-old Norway spruce affected by *Armillaria* root disease was reduced from one to six times compared with healthy trees (Sokolov 1964). Annual growth increment of diseased 80- to 120-year-old Norway spruce was about one-half that of healthy trees (Molin and Rennerfelt 1959). Kile and others (1982) observed reduced growth in messmate stringybark with over 25% of their root collar circumferences infected by *A. luteobubalina*. Norway spruce (110 years old) which were classified as heavily infected by *Armillaria* had wider growth rings early in the rotation than trees which were healthy or lightly infected (Hřib and others 1983). This suggests that faster growing trees become infected earlier and more frequently due to their more extensive root system and greater probability of contacting inoculum (Bloomberg and Reynolds 1985).

Later in the rotation, ring widths of trees in the two highest infection classes were 1 mm or less compared to 3 mm in uninfected trees (Hřib and others 1983). MacKenzie (1987) estimated volume loss of 6%-13% due to lethal and sublethal infection over a 28-year rotation of radiata pine. Growth loss due to *A. ostoyae* in 80- to 100-year-old Douglas-fir was measured on trees stratified by the proportion of the root collar showing resinosis (Bloomberg and Morrison 1989). Growth during 5-year periods, expressed as a percentage of the stem volume at the start of each period, decreased sig-

nificantly as resinosis increased due to colonization of the root system. In recently killed trees and in those with more than 50% basal circumference showing resinosis, growth began to decline 30 years previously. The volume increment of these trees during the last 5-year period was 10-50% less than that of healthy trees, depending on proportion of root system killed.

Twenty- to 40-year-old Norway spruces with butt rot had one-sided root distributions because *Armillaria* had killed one or more primary roots through which it had entered the stem early in the life of the tree. A reaction zone from which bacteria could be isolated extended as far as 50 cm up the stem (Yde-Andersen 1958). Butt rot of older Norway spruce was recorded by Molin and Rennerfelt (1959). In Britain, butt rot of conifers is commonly initiated when a small tap or sinker root is killed. The decay usually is limited to the lower 60 cm of the stem. Of species grown in Britain, Norway and Sitka spruces and western hemlock are most susceptible to butt rot while Douglas-fir, true firs, pines, and larches show considerable resistance (Gladman and Low 1963).

Armillaria root disease may kill its hosts by girdling the stem at the root collar. Prior to death, diseased trees may be windthrown due to decay of structural roots (Gladman and Low 1963, Shaw and Toes 1977), or they may be attractive to bark beetles which kill all or part of the tree (Cobb 1989).

Physiology of Symptom Development and Host Killing

The physiological basis of symptom development and host mortality is little understood for *Armillaria*, but two hypotheses have been proposed. First, symptoms develop as a direct result of the fungus physically disrupting the host's vascular system and the host's responses to it. Second, *Armillaria* species may produce metabolic toxins. The first hypothesis has been accepted by many investigators due to the nature of symptoms induced by *Armillaria*, particularly in the foliage. In mature conifers, shoot growth declines and the amount and color of foliage change gradually over several to many years as *Armillaria* destroys the host's vascular tissue. This view is supported by the results of Kile and others (1982), who found that patterns of electrical resistance were similar in mechanically girdled trees and those killed by *A. luteobubalina*. However, no experimental studies are known of host physiological parameters relative to location or extent of root system infection.

Several authors have postulated that symptoms are caused by a toxin produced by *Armillaria*. Orchard

trees affected by *Armillaria* appeared to exhibit symptoms of toxicity, possibly due to effects of metabolic products of the fungus (Zeller 1926). He suggested that branches died from toxic products since only branches above diseased roots showed symptoms, and pruning an infected root did not result in branch death. This view is supported by results of Thornberry and Ray (1953) who obtained a dark brown protein-like pigment from a liquid culture of *Armillaria*. The fungus had been isolated from a wilting peach tree. The substance induced wilting in tomato seedlings and peach twigs and penetrated 15-20 mm into vascular tissues. However, electrical resistance measurements around actively expanding lesions did not show that *A. luteobubalina* produces any systemic effects in eucalypts (Kile and others 1982).

Further research is needed to clarify the physiology and biochemistry of killing of host tissues (see chapters 3 and 7). Understanding this process could lead to characterization of pathogenic species and suggest what makes a host resistant to disease development.

Disease Diagnosis

Woody plants express diverse symptoms which may be categorized, in approximate chronological order, as follows: reduction of shoot growth, changes in foliage characteristics, crown dieback, stress-induced reproduction, basal stem indicators, and death. Generally, the nature of the symptoms and their rate of development relate to the position of attack and the rate of destruction of the host root system. If the disease progresses rapidly or the host is small, not all symptoms may be evident (Hartig 1874, Edgar and others 1976). Symptom development in conifers was more pronounced on vigorous hosts (Buckland 1953).

Above-Ground Symptoms on Individual Plants

Reduction of Shoot Growth

On conifer seedlings and trees up to about 10 years old, *Armillaria* rarely reduces shoot growth prior to death because killing occurs within a few months to a year after infection (Gibson 1960, Hartig 1874, Hintikka 1974). By contrast, the slower progress of the disease in older conifers causes a decline in shoot growth (fig. 5.9) which may be evident for many years (Molin and Rennerfelt 1959). In 80- to 100-year-old Douglas-fir, Bloomberg and Morrison (unpubl.) found terminal-shoot growth on diseased trees had declined for the previous 15-30 years. Actual time depended on the time since infection. Fruit trees affected by *Armillaria*

root disease may have a stunted appearance due to a shortening of internodes (Barss 1913, Cooley 1943).

Changes in Foliage Characteristics

On conifers which are killed quickly, foliage turns red or brown as it dries. When the disease progresses slowly, as in older trees, foliage gradually becomes stunted, chlorotic, and sparse (fig. 5.9). These changes usually occur throughout the crown (Hartig 1874, Molin and Rennerfelt 1959, Morrison 1981, Williams and others 1989). Symptoms in the crowns of young Douglas-firs are frequently accompanied by prolific resin blisters on the stem and branches (Buckland 1953).

Small hardwood trees frequently are killed so rapidly by *A. tabescens* that symptoms are not evident until the foliage withers and dies (Rhoads 1956) whereas the first indication of infection on larger trees is a thin crown with small leaves (Guillaumin 1977, Sokolov 1964). Trees later show gradual yellowing and defoliation followed by rapid wilting and dying of individual



FIGURE 5.9 — A 12-year-old Douglas-fir showing reduced shoot growth (for 2 years), chlorotic foliage, and a stress-induced cone crop. (D.J. Morrison)

limbs above diseased roots (Barss 1913, Bliss 1944, Rhoads 1956). On apple trees, premature defoliation is sometimes an indicator of *Armillaria* infection (Marsh 1952); and on diseased stone fruit trees, leaves roll along the mid-rib and wilt (Cooley 1943). Attacked by *A. luteobubalina*, eucalypt saplings up to 25 years old die suddenly (fig. 5.10), showing little deterioration of crowns before death (Edgar and others 1976). On older saplings, leaves show gradual reddening followed by browning and plant death (Pearce and others 1986). In pole-size to mature eucalypts, *A. luteobubalina* causes a general reduction in leaf density, drooping of foliage, epicormic shoots along branches, and eventually a dead top (fig. 5.11). Large trees which could not compartmentalize infections usually die 2-8 years after visible crown deterioration appears (Edgar and others 1976, Pearce and others 1986).

Crown Dieback

In pole-size to mature eucalypts attacked by *A. luteobubalina*, dieback of fine twigs and branches may lead to a dead top (Edgar and others 1976). Cooley (1943) observed that limbs on apple trees ceased growth and died on the same side as the affected root. Frequently, the combined action of *Armillaria* root disease and other biotic or abiotic agents has been associated with crown dieback and eventual mortality of many forest species, such as those noted in chapter 7 and table 8.3.



FIGURE 5.10 — A pole-stage mountain grey gum tree killed by *A. luteobubalina*. Little crown deterioration occurred prior to the sudden death of the tree. (G.A. Kile)



FIGURE 5.11 — Messmate stringybark trees showing stages in crown decline caused by *A. luteobubalina*. (G.A. Kile)

Stress-induced Reproduction

Many woody plants respond to advanced infection by producing a seed crop, usually in the season before death. Thus, tung oil trees produce nuts which are smaller than normal (Rhoads 1956), orchard trees produce poor, stunted fruit (Barss 1913), citrus trees develop an abnormally heavy bloom (Rhoads 1948), and conifers produce cones which are smaller but may be more numerous than normal (fig. 5.9) (Buckland 1953).

Basal Stem Indicators

Woody plants attacked by *Armillaria* frequently produce exudates or develop cankers, cracks, or flutes at or just above the root collar. Genera of conifers which normally have resin canals (*Pseudotsuga*, *Picea*, *Larix*, and *Pinus*) or which form traumatic resin canals (*Tsuga* and *Abies*) may produce resin that exudes through fissures (fig. 5.12) in the bark of the root collar and lower bole (Buckland 1953, Gibson 1960, Hartig 1874, Hintikka 1974, Rykowski 1975). Usually, resin exuda-



FIGURE 5.12 — Copious basal resinosis on a radiata pine attacked by *A. novae-zelandiae* or *A. limonea*. (C.G. Shaw III)

tion is not evident above-ground until the fungus is near or has reached the root collar. Responding to advanced *A. tabescens* attack, citrus trees occasionally (Rhoads 1948) and stone fruits commonly (Rhoads 1956) produce gum in the cambial region which may be so copious as to exude through cracks in the bark. Latex exudes from rubber trees at the root collar in the last stages of the disease (Riggenbach 1966). Exudation of kino through stem and root bark occurs on some mature eucalypt trees infected by *A. luteobubalina*; and from stems of trees less than 20 years old, it may be abundant, permeating and blackening the adjacent soil (Edgar and others 1976, Kile 1981).

Infections by *Armillaria* in 20- to 70-year-old Douglas-fir, white pine, and other conifers may be arrested after killing cambium at the root collar above a diseased root. Callusing occurs around the margin of the lesion. When fresh, lesions are resinous and have mycelial fans beneath the bark. Later, after the bark sloughs, the lesions can still be recognized by their short length, broad triangular shape, and the impressions of mycelial fans on the scar face (Molnar and McMinn 1960). Conical

basal scars on eucalypt stems (fig. 5.13) are frequently associated with *A. luteobubalina* infection (Kile 1981, Pearce and others 1986, Shearer and Tippet 1988). In citrus, basal lesions extend up to 35 cm above one or more diseased roots and may serve as entry points for other wood-rotting fungi (Rhoads 1948). The lesion at the base of some oil palms remains localized, dried, and apparently sealed off from the healthy tissue within; a mass of new roots forms above the canker (Wardlaw 1950). West African rubber trees infected with *Armillaria* or with *Rigidoporus lignosus* (Kl.) Imaz develop flutes at the stem base starting at the root collar near the point of infection (Riggenbach 1966).

A diagnostic symptom of *Armillaria* root disease on woody plants such as tea, coffee, and cacao in tropical or subtropical regions is the conspicuous longitudinal cracks that appear at the root collar and quickly extend up the trunk, hence, the name "collar crack" (Dade 1927). The cracks are longer and more numerous on the side of the tree where infection occurred. Similar cracks were observed on the roots and lower stem of citrus attacked by *A. tabescens* (Rhoads 1948) and on the roots of several hardwood species (Sokolov 1964).

In standing trees, heartwood decay (butt rot) does not produce external signs unless it is associated with a basal canker. In felled timber, butt rot caused by *Armillaria* may be recognized by characteristics of the decayed wood or confirmed by culturing. Where decay of structural roots is advanced in coniferous and broadleaved trees, they may be windthrown prior to death. This is particularly true where the tree is being sustained by adventitious roots.

Symptom Development in Relation to Extent of Colonization

The development of symptoms of *Armillaria* root disease in foliage and at the stem base depends upon the rate and degree of invasion of the host root system. Thus, on young (Gibson 1960, Swift 1968) or small trees (Rhoads 1956) in which the root system is invaded rapidly after infection, symptoms may appear just prior to death or only after the host is moribund. Death of radiata pine due to *A. novae-zelandiae* or *A. limonea* began 6 months after planting (MacKenzie and Shaw 1977). In 8- to 10-year-old plantations, an eastern white pine died 39 months after inoculation and a red pine infected by natural inoculum died 14 months after root examination showed it to be healthy (Patton and Riker 1959). On apricot trees, symptoms on aerial parts appeared only after the root collar was attacked or several large roots were killed (Guillaumin 1977); and on apple trees, girdling of the stem was complete 2-3 years after infection was first noted in one segment of the trunk (Marsh 1952).

Invasion of the root system of old or large trees usually occurs slowly over many years. Growth-ring studies on conifers 80 to 110 years old suggest that recently dead and severely affected trees became infected up to 50 years previously (Molin and Rennerfelt 1959). Consequently, symptoms develop gradually after a portion of the root system is colonized. Bliss (1944) found that *Armillaria* root disease was well established in citrus roots before any symptoms appeared in the crown. The fungus must reach the root collar before exudation of resin, gum, or kino becomes visible. More than half the root system of grand firs (mean age 50 years) had been killed by *Armillaria* with no apparent decline in tree vigor (Maloy and Gross 1963). Sokolov (1964) observed that the color and thickness of the crown and the incidence of cracks and resin flow on the lower bole were related to the proportion of first-order roots infected. In 80- to 100-year-old Douglas-firs, height growth reduction and the percentage of stem circumference showing basal resinosis were proportional to the amount of the root system colonized by *A. ostoyae* (Bloomberg and Morrison 1989). Crown symptoms on these trees were not obvious until one-half to three-quarters of the primary roots had been invaded. Crown dieback in-

creased with increasing root collar infection in eucalypts attacked by *A. luteobubalina* (Edgar and others 1976, Kile 1981); the height of infection on stems was positively correlated with circumference infected (Kile 1981).

Confirmation of *Armillaria* Occurrence

Many symptoms described above are non-specific; that is, they may be induced by a number of biotic and abiotic factors. To confirm *Armillaria* root disease, the root collar and lower bole of the tree must be examined for signs specific to the fungus. Those signs include mycelial fans, rhizomorphs, basidiomes, and decay. *Armillaria* may also be confirmed by culturing from the host. Many of the signs are useful for identifying stumps and roots which are within disease centers or on cutover sites, and which may be inoculum sources for the next rotation.

Mycelial Fans

On plants showing symptoms of advanced infection and on those recently killed, creamy-white mycelial sheets up to 10 mm thick occur in the cambial zone of roots and the lower bole (Greig and Strouts 1983, Morrison 1981, Williams and others 1989). The mycelial sheets, commonly known as fans and occasionally referred to as xylostroma, are the most useful diagnostic characteristic of *Armillaria* species in woody plants (figs. 5.14A,B). The mycelial fans of some *Armillaria* species are marked with perforations (fig. 5.15) 0.2-3 mm in diameter (Gibson and Corbett 1964, Kile and Old 1982, Rhoads 1945). In plants which have been dead for several years, mycelial fans usually can be found in roots below-ground but have disappeared from above-ground parts due to competing fungi or to unfavorable environmental conditions, such as desiccation. On conifers, impressions of fans in resin and bark may be present for several years after fans disappear (fig. 5.16).

Several reports of *Armillaria* on African crops (Dade 1927) and on hosts of *A. tabescens* in Florida (Rhoads 1948) refer to frills of xylostroma, at first cream-colored then becoming dark brown with age, which protrude from the longitudinal fissures in the bark. The description by Dade (1927) indicates that xylostroma sheets are extensions of subcortical mycelial fans which become melanized when exposed to air, an observation confirmed by Rhoads (1948).

Rhizomorphs

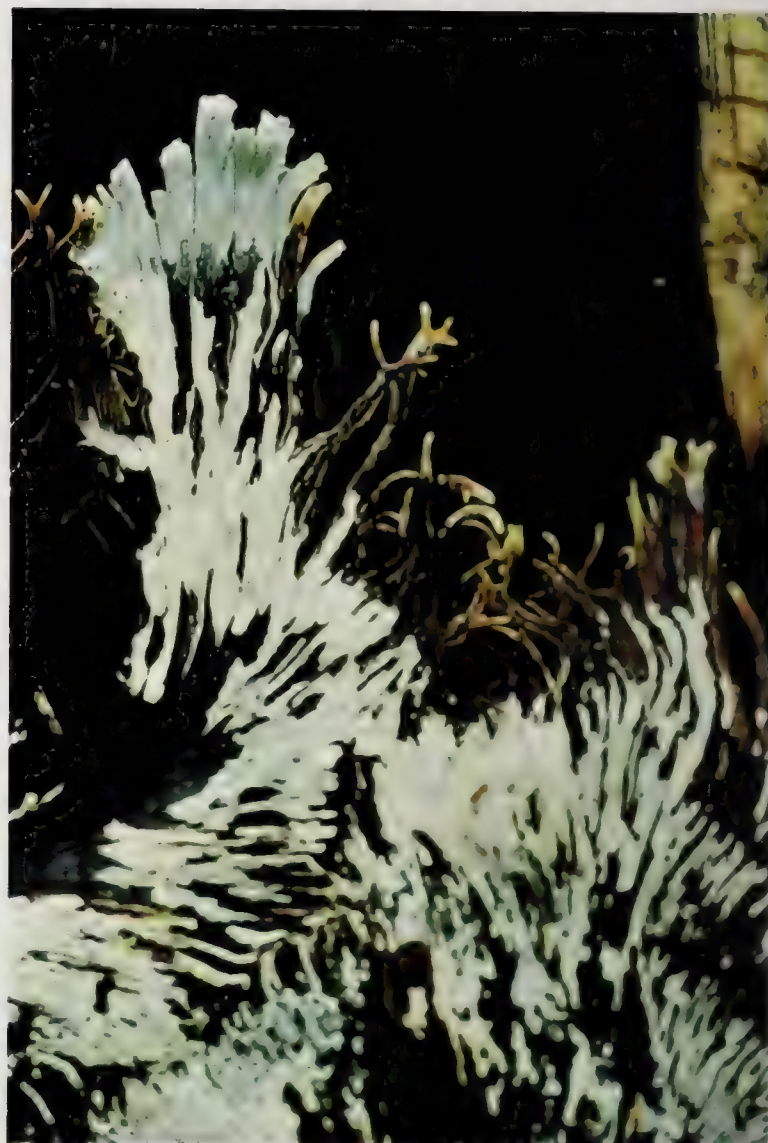
Rhizomorphs are initiated on the food base from the edges of mycelial fans, either subcortically when conditions such as loosening of bark prevents further growth



FIGURE 5.13 — Basal lesion on mountain grey gum caused by *A. luteobubalina*. (G.A. Kile)



A



B

FIGURE 5.14 — A: Mycelial fans of *A. ostoyae* in the cambial zone of an 8-year-old Douglas-fir. (D.J. Morrison). B: Mycelial fans of *A. luteobubalina* on brown barrell eucalypt. Note rhizomorphs emerging from the fan margin where the bark was loosened. (G.A. Kile)



FIGURE 5.15 — Perforated mycelial fans of *A. luteobubalina* developed in vitro in stem segments of silver wattle. (G.A. Kile)

of the fan (fig. 5.14), or into soil when the fan reaches the bark-soil interface (Morrison 1972). For up to 1 cm from the growing tip, a rhizomorph is white; with increasing distance from the tip it becomes red-brown,

brown, and finally black. A rhizomorph is hollow near the growing tip; however, within 2 cm, the hollow becomes filled with randomly arranged fiber hyphae in a mucilaginous matrix (Redfern 1973, Schmid and Liese 1970). Rhizomorphs in soil and on the surface of roots are usually 1-3 mm in diameter (Morrison 1972, Pearce and others 1986, Redfern 1973). Occasionally, rhizomorphs in soil, probably of *A. gallica*, are 5 mm in diameter (Redfern 1973). Rhizomorph structure is discussed fully in chapter 3.

In the north temperate zone (Greig and Strouts 1983, Wargo and Shaw 1985), New Zealand (Hood and Sandberg 1987), and at higher elevations in East Africa (Gibson 1960), India (Satyanarayana and others 1982) and Sri Lanka (Gadd 1930), rhizomorphs of *Armillaria* species grow freely through soil and on the surface of roots. The rate of growth and distance from the food base that they will grow varies greatly among species. Species with monopodially branched rhizomorphs, such as *A. gallica*, often produce extensive networks in

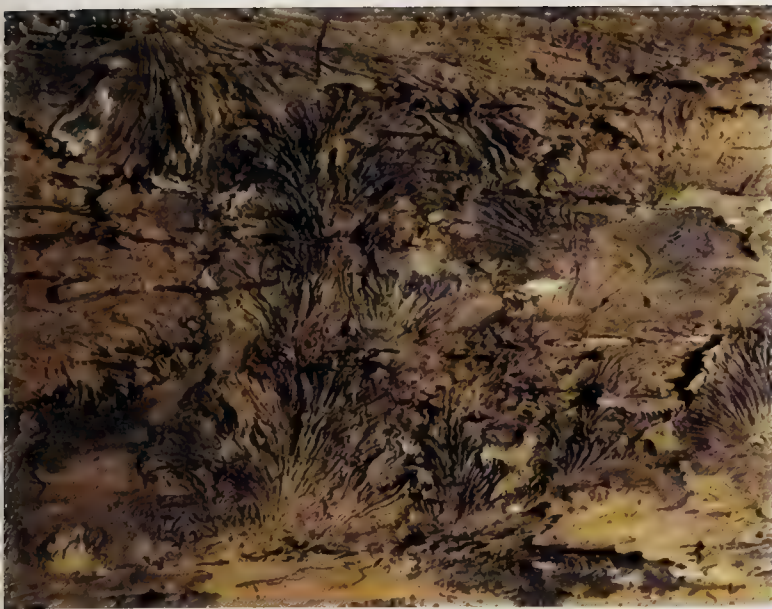


FIGURE 5.16 — Impressions of *A. ostoyae* mycelial fans on the inner bark of Douglas-fir. (D.J. Morrison)

soil, whereas dichotomously branched species, notably *A. mellea* (Rishbeth 1982), appear to be restricted to within a few centimeters of the food base. For this reason, the usefulness of rhizomorphs as a diagnostic feature is limited, particularly at the specific level.

At low elevations in the tropics, rhizomorphs are not found in soil or on roots (Dade 1927, Gibson 1960, Rishbeth 1980, Swift 1968), although occasionally they grow up to 2 cm into soil and then die (Dade 1927). In Australia, rhizomorphs either were not observed in the field (Kile 1981, Shearer and Tippet 1988) or were found only on the surface of roots (Kile 1980b, Pearce and others 1986).

Basidiomes

Basidiomes occur in clusters arising from mycelial fans in the host or in small numbers from rhizomorphs on the host or in soil. Basidiomes facilitate surveys of disease incidence (Pearce and others 1986) and identification of the *Armillaria* species (see chapter 1). Basidiomes often occur on or near hosts lacking other signs and symptoms. In temperate regions, fruiting occurs from mid-summer to mid-winter, depending on latitude and weather. Precipitation and favorable temperatures are required to initiate fruiting and for basidiome development. Basidiomes which develop slowly due to cold or dry weather may have short, thickened stipes and small thick pilei; weather may also affect basidiome color (Kile and Watling 1981). In tropical regions, basidiome formation varies from rare in Sri Lanka (Gadd 1930) and East and Central Africa (Wallace 1935, Gibson 1960b, Swift 1972) to common in West Africa (Dade 1927, Rikkenbach 1966), where it occurs almost exclusively in the wet season (Wardlaw 1950).

Decay

Armillaria species cause a white rot of woody tissues as lignin and cellulose both decompose. The appearance of decayed wood varies somewhat among hosts. In conifers, wood with incipient decay is stained gray to brown, often with a water-soaked appearance. Later, decayed wood becomes yellow-brown and stringy (figs. 5.17 and 5.18) and is finally reduced to a very wet, stringy rot with pale yellow flecks (Greig and Strouts 1983, Williams and others 1989). Decayed wood of broadleaved hosts is watersoaked and white to yellow, becoming spongy and ultimately distinctly gelatinous (Greig and Strouts 1983, Rhoads 1956).

Pseudosclerotial plates (zone lines) are common in woody tissues decayed by *Armillaria* species (Campbell 1934, Lopez-Real 1975, Greig and Strouts 1983, Podger and others 1978). These plates are composed of pigmented bladder hyphae which are identical with the cells comprising the outer coat (rind) of mature rhizomorphs (Campbell 1934, Lopez-Real 1975). Wood decayed by some, but not all, *Armillaria* species is bioluminescent (Kile 1980b, Podger and others 1978). The biochemistry of bioluminescence is discussed in chapter 3.

Isolation Technique and Appearance in Culture

The presence of an *Armillaria* species in host tissue may be confirmed by culturing colonized bark or wood or subcortical mycelium on a medium such as potato dextrose or malt extract agar. Molds or bacteria may be suppressed by acidifying the medium or amending it with a fungicide such as o-phenylphenol (Russell 1956) or benomyl (Hunt and Cobb 1971, Maloy 1974). Isolation of *Armillaria* from root tissues of dead and dying trees increased by 40% on malt agar amended with o-phenylphenol (Whitney and others 1978). The selective media developed by Kuhlman (1966) and Kuhlman and Hendrix (1962) for isolating *H. annosum* from wood and its spores from soil also is selective for *Armillaria* (Shaw 1981a). The fungus may be isolated from rhizomorphs by first washing short lengths in water then soaking them in 10% hypochlorite for 5 min (Rishbeth 1978b). Hood and Sandberg (1987) made isolations from rhizomorphs after dipping them in 95% ethanol, surface sterilizing in 10% hydrogen peroxide, and washing in distilled water.

Nobles (1948) suggested that *Armillaria* cultures are recognizable from macroscopic appearance alone, their red-brown crustose areas, rhizomorphs, and frequent luminosity of young, actively growing colonies being unique. Her description is based on four isolates, three of which were from conifers in British Columbia and



FIGURE 5.17 — Yellow stringy decay of Douglas-fir root wood caused by *A. ostoyae*. (D.J. Morrison)



FIGURE 5.18 — *Armillaria*-caused butt rot of Norway spruce. (B.J.W. Greig)

Washington. It is likely that the description is based on cultures of *A. ostoyae*. However, these features are characteristic of most, if not all, species of *Armillaria*. Differentiation of vegetative isolates of *Armillaria* is discussed in chapters 1 and 2.

Biotic and Abiotic Conditions Causing Similar Symptoms

Any agent or condition which affects the root system of a woody plant may cause some or all of the symptoms described above. In conifers, root diseases caused by *H. annosum* (Greig and Redfern 1974), *Phellinus weirii* (Murr.) Gilbn. (Thies 1984, Wallis 1976), *Inonotus tomentosus* (Fr.) Teng (Whitney 1978a) and *Leptographium* spp. (Wingfield and others 1988) may cause crown symptoms similar to those of *Armillaria*. On apple trees, winter injury to the roots or root collar or root suffocation due to flooding can induce symptoms similar to *Armillaria* root disease (Cooley 1943). Stem girdling or root killing due to any cause induces foliage symptoms in citrus similar to those of *Armillaria* root disease (Rhoads 1948).

Disease Detection

Detecting *Armillaria* root disease in production forests, amenity woodlands, and agricultural plantations depends on observable symptoms in the crown and on the stem base plus signs of the fungus such as mycelial fans, rhizomorphs, and basidiomes on the host. Diseased trees occur as scattered individuals or in centers which reflect the distribution of the *Armillaria* species. Characteristics of disease centers are discussed in chapters 8, 9, and 10.

Aerial photography and ground surveys conducted independently or in combination have been used to detect root diseases, including those caused by *Armillaria*. Choice of survey method is influenced by the purpose of the survey. For example, the survey may intend to determine presence or absence of root disease, estimate wood volume in diseased trees, delineate distribution of disease, or provide input data for modeling purposes (see chapter 10). Aerial photographs (Kable 1974) and stem maps (Marsh 1952) also have been used to detect and record progress of *Armillaria* root disease in agricultural plantations.

Using aerial photography permits large areas of forest to be inspected rapidly for visibly affected trees, for quantifying effects, and for providing a record of disease occurrence. Some ground inspection is required to identify the pathogenic species involved and to verify the photographic assessment. The choices of image scale and film emulsion to be used are based on stand structure, ease of defining disease signature, and purpose of the imagery. While detection of disease centers and affected single trees may be accomplished at scales up to 1:10000 (Gregg and others 1978, Murtha 1972, Myers and others 1983, Williams 1973), larger scale imagery, 1:1000-1:2000, may be necessary to provide rea-

onable accuracy in delineating areas affected. Generally, relatively large scale imagery, 1:3000-1:6000, is most often used for detecting and quantifying individual trees or centers (Gregg and others 1978, Myers and others 1983, Wallis and Lee 1984, Williams 1973, Williams and Leaphart 1978). Color and false color (color infrared) emulsions are frequently used (Gregg and others 1978, Heller and Bega 1973, Williams and Leaphart 1978); black and white may also be effective (Johnson and Wear 1975).

In western North America, the signature of root disease centers on aerial photographs included openings in the forest canopy with dead or nearly dead standing trees on the margins, snags, and windthrown conifers, and generally a shrub cover and some young trees in the opening (Wallis and Lee 1984, Williams and Leaphart 1978). Dead trees and crown decline characterized *A. luteobubalina* centers on photographs of jarrah forests in Western Australia (Shearer and Tippett 1988).

Ground evaluations using various survey procedures are efficient if areas are small or if precise disease location and damage measurements are required. Survey design varies from regularly or randomly spaced transects to systematically spaced variable and fixed-radius plots (Jacobi and others 1981). Pearce and others (1986) used random reconnaissance, transect and plot surveys to determine the occurrence of basidiomes and the incidence of infection in stumps, saplings, and trees. The ground survey method developed for *P. veirii* (Bloomberg and others 1980a,b) and modifications for multiple-disease recording and stratification by infection intensity (Bloomberg 1983) are applicable to surveys for *Armillaria* root disease. This transect sampling system involves randomly located sets (grids) of lines to estimate the incidence, distribution, and area of root disease. Estimates of diseased area are derived from length of transect intersecting root disease centers and probability of occurrence. Random location of gridlines in a stand results in independent estimates for each grid, hence the variance of their means can be estimated.

The Bloomberg method is difficult to apply in logged, burned, or open stands with diffuse disease distribution because locating infection boundaries can be diffi-

cult. For that reason, Kellas and others (1987) used systematically located transects with variable-sized plots around selected stumps to assess infection by *A. luteobubalina* in regeneration, regrowth, and overwood trees. Incidence and severity of *Armillaria* root disease can be assessed during inventory surveys (B. Geils, unpubl.). Ground survey data such as that frequently collected by the USDA Forest Service (1986) may be used to initialize a model of *Armillaria* root disease (see chapter 10), if augmented to include stumps infected with root disease (Stage and others 1990).

Where survey information is required for large areas, multi-stage or double sampling designs incorporating aerial photography and ground evaluations can be employed (Stewart and others 1982, Williams and Leaphart 1978, Wood 1983).

Conclusions

The infection process has been observed on hardwood and coniferous hosts. Post-infection disease development has been observed for a few host species but not throughout a rotation. The response to infection by a variety of host species has been recorded, primarily at the macroscopic level, but less is known of the interactions between hosts and *Armillaria* at the biochemical level. The effects of *Armillaria* root diseases on their hosts, growth loss, decay, and mortality, are known. Symptoms of *Armillaria* root diseases which are non-specific include reduction of shoot growth, changes in foliage characteristics, crown dieback, stress-induced reproduction, basal stem indicators, and death. Signs specific to *Armillaria* species are subcortical mycelial fans, rhizomorphs, and basidiomes. Cultures of *Armillaria* have distinctive characteristics. Ground and aerial methods for detecting *Armillaria* root diseases and ground procedures for determining disease area have been developed although work is needed to improve their utility. Understanding the biochemistry and physiology of the host-parasite interaction and studies of disease development during a rotation for representative combinations of host and *Armillaria* species remain the most urgent research needs relating to infection and disease development.

Pathogenicity and Virulence

Steve C. Gregory, John Rishbeth, and Charles G. Shaw III

The terms pathogenicity and virulence both refer to an ability to cause disease. That "*Armillaria mellea*" can cause disease has been known for over a century, but its propensity to do so has been a matter of controversy. Rhizomorphs commonly surround tree roots without infecting them, yet *Armillaria* may cause extensive mortality elsewhere in the same area. Such observations were interpreted by some early authors as indicating that trees in affected areas were weakened or predisposed to infection in some way (Day 1927b, 1929). Others, for example Piper and Fletcher (1903) and Childs and Zeller (1929), proposed that there were several forms of the pathogen that differed in virulence.

According to the former view, *Armillaria* was a secondary pathogen capable of attacking only trees with lowered resistance. Thus, Day (1929) concluded that "all the evidence goes to show that it is always secondary to some other factor acting as a primary cause of disease." Boyce (1961) stated that the fungus "does not attack thrifty trees" and Gremmen (1976) expressed the view that "control of *A. mellea* in forestry ... has no effect since the fungus is not the primary cause of die-back." Contrary to these assertions, however, there are early accounts of *Armillaria* disease (for example Hendrickson 1925, Zeller 1926) that describe attacks by a fungus with every appearance of a "virulent primary pathogen," as it was termed by Patton and Riker (1959). Dade (1927) similarly described the behavior of "*Armillaria mellea*" in tropical West Africa, and Brooks (1928) regarded it as "perhaps the most dangerous subterranean parasite of trees, bushes and certain herbaceous plants."

Many contradictions regarding the pathogenic behavior of "*Armillaria mellea*" can now be understood as having arisen from observations made on different *Armillaria* species. They can differ markedly in pathogenicity yet closely resemble each other in the appear-

ance of their basidiomes, rhizomorphs, and mycelial sheets. The extremely low pathogenicity of some species may partly explain the dismissive attitude some earlier authors held toward *Armillaria* as a pathogen.

Pathogenicity, Virulence, and Disease

Distinguishing between pathogenicity and virulence is especially important when so many species and so many different hosts are involved. "Pathogenicity" means the quality or characteristic of being able to cause disease as applied to a genus or species (British Federation of Plant Pathologists 1973). "Virulence" means the observed infective capacity of individual entities of a pathogenic species (British Federation of Plant Pathologists 1973).

Pathogenicity of an *Armillaria* species was first established in an inoculation experiment by Hartig (1874) though his method fell short of satisfying Koch's postulates, which are now generally accepted as the requirements for proving pathogenicity (British Federation of Plant Pathologists 1973). An extensive world literature on *Armillaria* now contains enough data from inoculation experiments to leave no doubt that several pathogens occur in the genus.

Some physiological attributes of the fungus that may be associated with high or low virulence are discussed in chapter 3, but the genetic basis of virulence in *Armillaria* is largely unknown. Two studies have shown that haploid isolates derived from single basidiospores may display high virulence, in some cases as high as the parent isolate (Raabe 1972, Shaw and Loopstra 1988). The wider genetic significance of this finding and its relevance to field behavior remain to be investigated. Reaves and others (1988) suggested that the occurrence of virus-like particles in the cytoplasm of some *Armillaria* isolates might be associated with high virulence, but little evidence supports this hypothesis.

Saprophytic and Parasitic Behavior

Armillaria species have both saprophytic and parasitic phases in their life cycle, but distinguishing the two may be difficult in an activity such as colonization of a moribund stump. By causing root- and butt-rot in standing trees, *Armillaria* species can also be classified as perthophytes because they utilize dead tissues in living hosts (British Federation of Plant Pathologists 1973). Most of the methods of capturing resources for saprophytic or perthophytic exploitation that have been outlined in chapter 4 depend on the fungus' abilities as a parasite even though the tissues involved might be of extremely low vigor, as in stumps and dying trees.

Pathologists and mycologists now recognize that *Armillaria* species differ markedly in pathogenicity. Highly pathogenic species survive saprophytically in the hosts they kill through their parasitic activities, whereas weak pathogens probably exist for the most part as saprophytes or possibly perthophytes (Korhonen 1978, Rishbeth 1985a, Wargo and Shaw 1985). This diversity poses the question whether weakly pathogenic species are better able than highly pathogenic species to colonize moribund tissues and compete with saprophytic micro-organisms. Little information is available on this subject, and it is clearly an area that merits further research.

Rishbeth's (1985a,b) experiments with excised root and stem material demonstrated that, in some circumstances at least, the weak pathogen *A. gallica* is no more capable than the highly pathogenic *A. mellea* of colonizing woody material with residual host resistance and may even have an inferior ability to penetrate intact bark on such material. The same studies suggest that these two species may differ little in their ability to colonize completely dead material, and both may possess considerable competitive saprophytic ability (*sensu* Garrett 1956a, 1970).

Armillaria ostoyae, another highly pathogenic species, did not perform as well as *A. mellea* and *A. gallica* in Rishbeth's (1985a,b) tests with excised material. In western North America *A. ostoyae* is considered incapable of colonizing stumps that were not already infected as living trees (Filip 1989a). Although it is one of the assumptions underlying recent models of disease development (see chapter 10; McNamee and others 1989), the reasons for this apparent inability are not clear. It may reflect the species' limited capacity for spreading by rhizomorphs as much as any deficiency as a saprophytic competitor.

An important attribute of weakly pathogenic species is an ability to act as facultative parasites on stressed or sickly hosts (Kile 1980b, Rishbeth 1985a, Wargo and

Shaw 1985). However, many observations suggest that highly pathogenic species are also capable of invading weakened hosts (Davidson and Rishbeth 1988, Dumas 1988, Gregory 1989, Guillaumin and others 1989a, Rishbeth 1985a). In nature, it is probable that the weakly pathogenic species more often do so (Kile 1980b, Kile and Watling 1983, Rishbeth 1982).

Quite possibly, some of the less pathogenic *Armillaria* species have evolved strategies, such as rhizomorph behavior, that confer advantage of position in exploitative situations (Gregory 1985, Rishbeth 1985a, Wargo 1984b, see chapter 4). Indeed, the paucity of data permits more general speculation that the undoubted success of such species owes less to any greater ability to penetrate and invade weakened or dead tissues than to an ecology that affords them the maximum opportunity to encounter such material. This is more fully discussed in other chapters, but it is relevant to note here that such considerations necessitate great caution in interpreting observations and experiments on pathogenic behavior.

Conditions For Disease

Implicit in the definition of pathogenicity is the qualification that measurement should be made under specified conditions. Among the most important elements that may influence the expression of pathogenicity are the host, the external environment, and the nutrition of the pathogen. Pathogen nutrition is contained in the concept of inoculum potential which was elaborated by Garrett (1956a, 1970). The ability of a pathogen, whatever its inherent virulence, to cause disease is strongly influenced by the energy available to it at the host surface. The subject of inoculum potential is discussed in chapter 4.

Host resistance is an important constraint on disease, and many studies have shown that susceptibility to *Armillaria* disease differs among host species. European forest hardwoods have been shown to possess considerably more resistance than native or exotic conifers (Redfern 1978, Rishbeth 1984), results that are in accord with most field observations. However, some conifers are notably resistant (Guillaumin and Pierson 1978) and some hardwood genera, *Prunus* and *Citrus*, for example, are notoriously susceptible (Guillaumin and Pierson 1978, Raabe 1967, Wilbur and others 1972). Differences in susceptibility of woody species within individual genera have frequently been demonstrated (Benjamin and Newhook 1984b, Guillaumin and others 1989b, Proffer and others 1988); and Azevedo (1970-71) found that two forms of the same species (Japanese redcedar) also differed.

Host resistance is not only a genetic attribute but also a result of circumstances. Notwithstanding the historic controversy over the role of host predisposition in *Armillaria* pathogenesis, factors associated with low host resistance will favor disease. Good circumstantial evidence from several parts of the world indicates young trees are more prone to infection than older trees of the same species (Gibson 1960, Ono 1970, Pearce and others 1986, Redfern 1978), and many pathologists believe stress imposed by ill-health, injury, or unsuitable growing conditions can increase susceptibility (see chapter 7).

The best known limitations imposed by the external environment on the activities of pathogenic *Armillaria* species are the effects of soil on rhizomorph growth and production. The complicated relationships between rhizomorphs and disease are discussed briefly in the following sections and more fully in chapter 4.

Decay and Disease

The commonly accepted definitions of disease refer to deviation from normal functioning of physiological processes (British Federation of Plant Pathologists 1973). It is therefore arguable whether butt rot, which involves the decay of largely non-living interior wood in living trees, constitutes disease. We will accept it as such since living cells in the wood are likely to be affected to some degree in many cases. The ability of *Armillaria* species to cause decay in standing trees is therefore an expression of pathogenicity though it appears not to have been investigated experimentally. Most experiments assess virulence entirely by the effects of the pathogen's development in the phloem and cambium.

In practice, root killing and root decay are often not clearly separable since one closely follows the other. Nevertheless, these processes involve the capacity to invade and exploit two quite different tissues, and the decay-causing ability of an isolate is not necessarily related to its capability as an agent of tree mortality. Decay has been little studied in *Armillaria*, but field observations in Europe (Gregory 1989, Korhonen 1978, Rishbeth 1982) suggest that species with limited ability to kill trees are associated with butt rot at least as often as highly pathogenic species.

Host Specialization

Many *Armillaria* species have a wide host range, both among the genera which occur naturally in their habitat and among exotics. For example, the Australian species *A. luteobubalina* not only attacks many native tree and shrub species in many genera but is also highly pathogenic to some North American conifers

(see chapter 8; Morrison 1989). Such behavior does not preclude the existence of adaptive relationships between particular pathogens and particular hosts ("host specialization" or "host preference"), though few have been clearly demonstrated in *Armillaria*. In Europe, the area from which most data are available, *A. ostoyae* appears to be better adapted to coniferous hosts and *A. mellea* to hardwoods (Guillaumin and others 1985; Guillaumin and Lung 1985; Guillaumin and others 1989a; Rishbeth 1985a; Siepmann 1985). However, distinguishing the effects of host specialization from those of site history and pathogen ecology is often difficult. Both may limit the opportunities for contact between the fungus and some potential hosts.

Assessing Pathogenicity and Virulence

The ability to cause disease can be estimated from direct measurement of the amount of disease actually caused in inoculation trials, observation of field behavior, or an assay of some feature thought to be associated with the pathogen's ability to cause disease. All three approaches have been attempted with *Armillaria*, but the first two have undoubtedly been the most useful.

As already discussed, the intrinsic ability of an *Armillaria* species to cause disease may be modified by circumstances and environment. Hence, inoculation trials must be conducted under specified conditions, choice of which is exceptionally difficult with tree-root pathogens, such as *Armillaria*, that have a wide host range and that can attack trees of virtually any age. Moreover, the infection of such a massive and well-protected structure as a woody root requires a specialized pathogen (*sensu* Garrett 1970) for which the method of infection, and particularly the necessary inoculum potential, may be difficult to achieve artificially. For many *Armillaria* species, the chief means of infection is the rhizomorph, a specialized structure that may develop only under certain conditions and the efficacy of which is governed partly by the energy supplied to the infective tip (Garrett 1956b).

Choice of Host for Inoculation Trials

Most investigators have selected trees or shrubs for pathogenicity trials. However, some have attempted to avoid the considerable difficulties of experimentation with intact woody hosts by using parts of plants or plant organs which may possess much less host resistance than a tree but might retain enough to repel isolates of low virulence.

Large vegetable roots and tubers have proved valuable subjects for the study of infection biology. Garrett (1956b), Thomas (1934), and van Vloten (1936) used

potato tubers to demonstrate apparent differences in virulence between *Armillaria* isolates. Gregory (1984, 1985) and Rishbeth (1984) also attempted to use potato tubers to test virulence, comparing the results obtained with them to those obtained by using the same isolates on young trees. Although Gregory (1984, 1985) found some correspondence, infection of the tubers generally occurred too readily for it to be pursued as a useful discriminatory method.

The dangers of using material with low host resistance for determining the virulence of *Armillaria* isolates may be increased when the "host" is an excised root or stem. The ability to colonize moribund material may be of equal evolutionary advantage, and hence as well developed, in pathogens of low virulence as in those of high virulence. As discussed by Rishbeth (1985a,b), there is compelling evidence that *Armillaria* species of low pathogenicity can successfully colonize such material both in nature and in the laboratory. Indeed, the commonly used method of preparing inocula developed by Redfern (1970, 1975) depends on this very ability. Rishbeth (1984) compared the ability of several isolates to colonize excised stems and roots. His results did not encourage the use of this ability as a measure of virulence since isolates of *A. gallica* generally performed better than those of *A. ostoyae*, a reversal of the normal ranking for pathogenicity.

Among workers who have used trees or shrubs for pathogenicity tests, many have chosen to include more than one species because of known or suspected differences in susceptibility among potential hosts (Benjamin and Newhook 1984b, Guillaumin and Lung 1985, Guillaumin and Pierson 1978, Kile 1980b, Morrison 1982b, Mugala and others 1989, Proffer and others 1988, Raabe 1967, Rishbeth 1985b, Shaw and Loopstra 1988). Other investigators have confined themselves to a host in which *Armillaria* is a current economic problem (Leach 1937, Mallett and Hiratsuka 1988, Ono 1970, Podger and others 1978, Wilbur and others 1972). The type, age, and method of cultivating experimental subjects have differed greatly, but four plant types have been commonly used: very young seedlings grown under laboratory conditions, potted plants, plants in field plots, and established trees.

Several attempts have been made to use seedlings under sterile or near-sterile conditions for laboratory infection studies (Christensen 1938, Irvine and McNabb 1962, Rayner 1930, Rishbeth 1984, Zollfrank and Hock 1987). In these experiments, infection either hardly occurred at all (Christensen 1938, Rayner 1930, Rishbeth 1984) or was achieved only by growing the seedlings in a culture medium permeated by the fungus (Irvine and McNabb 1962, Zollfrank and Hock 1987). The symptoms reported in some cases do not

resemble those that occur in the field (Rayner 1930, Zollfrank and Hock 1987). Laboratory methods inevitably limit host size and the type of inoculum that can be used, so results must be considered as bearing little relationship to pathogenesis in vivo.

Inoculating young trees in containers (figs. 6.1, 6.2) has, by contrast, provided much valuable information on the infection biology and pathogenicity of *Armillaria*. In North America, this method contributed to several important studies of "*Armillaria mellea*" (Bliss 1946; Patton and Riker 1959; Raabe 1955, 1967, 1972; Shaw 1977; Thomas 1934), and it formed the basis of several recent investigations into the pathogenicity of the currently recognized North American species (Mallett and Hiratsuka 1988, Morrison 1989, Mugala and others 1989, Proffer and others 1988, Shaw and Loopstra 1988). European, Asian, and Australasian studies have also made extensive use of container plants (Gregory 1985; Guillaumin and Lung 1985; Guillaumin and Rykowski 1980; Kile 1980b, 1981; Ono 1970; Pearce and others 1986; Podger and others 1978; Redfern 1978; Shaw and others 1980, 1981; Siepmann and Leibiger 1989). Several workers (Morrison 1989; Ono 1970; Redfern 1975, 1978; Pearce and others 1986; Proffer and others 1988) have used several plants per container with each container being treated as a plot.

Experimental field plots established in open ground have also been used effectively in *Armillaria* research. Most experimental data on virulence of European isolates derive from the field plot inoculations of Rishbeth



Figure 6.1 — Inoculation of a ponderosa pine seedling with a branch segment of red alder containing *A. ostoyae* (see Shaw 1975, 1977). The jar contains inoculum segments on which *A. ostoyae* mycelium is visible as white tufts. (G. M. Filip)



Figure 6.2 — Two treatments from Redfern's (1975) trial, photographed 18 months after inoculation with European isolates of *A. gallica* (S3) and *A. mellea* (S4) in root segments of planetree. Each container originally held 25 young Sitka spruce. *A. mellea* (S4) killed all but a few plants in this replicate (treatment total of 61%), whereas *A. gallica* (S3) killed none (less than 5% over the whole experiment). (D. B. Redfern)

(1982, 1984, 1985a,b) who primarily used 2-year-old Scots pine but also worked with other conifers and a range of hardwood trees and shrubs. Guillaumin and Pierson (1978) used 4- to 5-year-old specimens of peach, Persian walnut, downy oak, and silver fir in field trials in France. In the United States, Wilbur and others (1972) used field plots of peach. One of the few inoculation trials to have been reported for an African *Armillaria* isolate was conducted in a field plot of common tea seedlings by Leach (1937).

Relatively few inoculations of established plantation or forest trees have been reported though the hosts for the earliest recorded inoculation were 8-year-old pines in Germany (Hartig 1874). One of the first demonstrations that "*Armillaria mellea*" exhibited differences in virulence was achieved by inoculating young plantation pines in the United States (Patton and Riker 1959). Also in the United States, there has been a history of field inoculations in research on *A. tabescens* (Plakidas 1941, Rhoads 1956, Weaver 1974). The pathogenicity of two other species has been proven by field inoculation. Kile (1981) inoculated young eucalypts with *A. luteobubalina* in Australia, and Dadant (1963a) inoculated field-grown albizia with *A. fuscipes* in Madagascar. Large woodland trees have been inoculated in several other studies in which the objective was investigation of host-parasite relationships rather than straightforward testing of pathogenicity (Davidson and Rishbeth 1988, Redfern 1978, Wargo and Houston 1974, Whitney and others 1989b).

Inoculating forest or plantation trees could yield data more relevant to field experience than any other method discussed in this section. However, the practical difficulties involved are often formidable. Using containers offers ease of handling, flexibility of experimental design, and greater freedom in environmental control, but conditions in containers, even those as large as Ono (1970) and Redfern (1975, 1978) used, can be quite artificial, particularly the rooting environment. Any stress imposed by such conditions could lower host resistance and might thereby obscure differences in virulence between isolates. As noted elsewhere in this chapter, some species of *Armillaria* with limited ability as primary pathogens can nevertheless act as effective secondary pathogens on weakened trees. Conditions in containers, such as extremes of soil moisture, also may adversely affect the fungus (Guillaumin and Leprince 1979).

Growing conditions in field plots are clearly more natural than those in containers though trees are not necessarily stress-free. Morrison (1982b) mentioned drought stress as a possible factor contributing to high infection in plots established on a sandy soil. Conversely, one cannot assume that artificial or unnatural conditions are always detrimental to the host. Well-tended plants in pots or field plots may be less prone to stress, and hence potentially more resistant, than trees of the same age in some natural situations.

Container plants are usually young and are therefore likely to be less resistant to infection and killing than older trees, an obvious drawback to applying results to the field. In most pot trials, experimental plants have been seedlings, cuttings, or transplants 1-4 years old at inoculation. Exceptionally, seedlings only a few weeks old have been used (Entry and others 1986) but results in such cases are likely to have little relevance to field behavior. Field plots offer greater opportunity for using older plants, though in many such studies age at inoculation has been 5 years or less (Guillaumin and Pierson 1978; Morrison 1982b; Ono 1970; Rishbeth 1982, 1984; Rykowski 1984).

Rishbeth (unpubl.) used a range of isolates and *Armillaria* species to inoculate, in parallel trials, 1-year-old plants in pots, 2-year-old plants in field plots, and 7-year-old plantation trees of Corsican pine. Although no true comparison was possible, the data suggest that isolates of low virulence could receive higher ranking from the results of trials with young potted plants than would be justified by other methods, including field observation. Results presented by Proffer and others (1988) are also of interest in this connection. They found uniformly high mortality in cherry (*Prunus*)

seedlings inoculated with one of three *Armillaria* species including *A. gallica*, which is normally regarded as an extremely weak pathogen. Quite possibly the isolate used was of exceptionally high virulence, but more likely, the methodology gave a spuriously high result. The hosts were 1-year-old seedlings to which inocula were attached at the time of planting. As the trial ran for only 1 year, both stress of transplantation and the young age of the plants might have increased susceptibility. The large amount of inoculum used per plant was another possible factor identified by the authors.

Choice of Inoculum

Garrett's (1956a) development of the concept of inoculum potential was founded on the recognition that failure to achieve experimental infection with root pathogens was often the result of using unsuitable inocula. As discussed in chapter 4, the inoculum potential for *Armillaria* pathogenesis in vivo is almost exclusively derived from woody substrates. Accordingly, although successful inoculations of young trees have been achieved with other material, the main experimental contributions to our knowledge of *Armillaria* pathogenicity and virulence have been based on the use of woody inocula.

Some workers have used naturally infected roots (Kile 1980b, 1981; Leach 1937; Ono 1970; Proffer and others 1988; Rhoads 1938), but these are of limited value for comparative work because of the uncertainty that uniform colonization has been achieved by a single isolate. Most investigators, including some of the earliest to conduct successful inoculation experiments, have used sterilized wood pieces inoculated with pure cultures of the isolates under investigation (Bliss 1946, Guillaumin 1977, Patton and Riker 1959, Podger and others 1978, Raabe 1955, Rishbeth 1984, Shaw 1977, Thomas 1934, van Vloten 1936, Wilbur and others 1972). Some have used inocula prepared in this way to infect live stem or root pieces which have then been used to inoculate the experimental plants (Gregory 1985; Redfern 1970, 1975, 1978; Rishbeth 1972b, 1982; Siepmann and Leibiger 1989). This two-stage method has proved advantageous with some isolates that do not readily produce rhizomorphs from sterilized wood (Redfern 1970). Both methods are time-consuming because inocula take many weeks to become completely colonized, the stage at which they are usually used (Podger and others 1978, Redfern 1975, Shaw 1977). Wilbur and others (1972) incubated inocula for as long as 20 months before use. The consequences of using inocula too early have been noted by Benjamin and Newhook (1984b) who found that incompletely colonized inocula did not produce rhizomorphs and that the colonization rate varied greatly among the several types of wood that they tried. Rhizomorph production can be an impor-

tant factor in achieving artificial infection, as will be discussed below, and it may be influenced directly by the food base used (Azevedo 1970-71; Morrison 1972; Redfern 1970; Rishbeth 1972b; Rykowski 1981c, 1984).

Redfern (1975) demonstrated that food base type can affect the amount of experimentally induced disease independently of how it affects the number of rhizomorphs. Choice of wood species for inocula is therefore potentially important for experimentation though the criteria used have rarely been stated. Several authors have used standard hardwood inocula for a range of hosts (Guillaumin and Lung 1985, Guillaumin and Pierson 1978, Raabe 1967, Rishbeth 1984, Shaw 1977, Shaw and others 1981, Siepmann and Leibiger 1989); Pearce and others (1986) used two different types for each host. Other workers matched inoculum to host (Dadant 1963a, Ono 1970, Podger and others 1978, Proffer and others 1988), or used unrelated species that are a common source of infection in nature (Leach 1937), or material that can be conveniently collected (Mallett and Hiratsuka 1988). The popularity of hardwood inocula even for coniferous hosts may well reflect the widespread view that hardwoods offer a superior food base for *Armillaria* species (see chapter 4; Redfern 1970, 1975).

The relative merits of using root, branch, or stem wood for inocula have received little attention although the origin could conceivably affect the fungus' pathogenic behavior. Several workers have used root segments (Dadant 1963a, Ono 1970, Patton and Riker 1959, Redfern 1975, Weaver 1974, Wilbur and others 1972), presumably reflecting the most common inoculum source in nature, but many others have achieved worthwhile results with stem or branch material (Gregory 1985, Guillaumin and Pierson 1978, Kile 1981, Morrison 1982b, Raabe 1967, Rishbeth 1982, Rykowski 1984, Shaw 1977).

The size of inocula and their positioning relative to the host have been little discussed despite Garrett's (1956b) early demonstration that both factors affect the ability of rhizomorphs to cause infection. Harrington and others (1989) and Patton and Riker (1959) attributed disappointing results in their field inoculations to under-sized inocula. Size influenced infection in Azevedo's (1970-71) and Rykowski's (1981c, 1984) experiments with young trees, but the latter still achieved infection of 3-year-old pines with inocula less than 5 cm³. Gregory (1985) and Guillaumin and Pierson (1978) conducted successful pathogenicity trials with comparatively small inocula (1.5-2 cm diam x 4-5 cm long) used singly and placed close to the collar or major roots of the host. Other workers have generally used larger inoculum segments and several have used more than one per host. Redfern (1975) used five large segments

(2.5-5.5 cm diam x 10 cm long) in each tub (30 cm diam) of 25 small conifers, whereas Davidson and Rishbeth (1988) used similarly sized inoculum segments singly to attempt inoculation of 32-year-old oak trees. Leach (1937) used a massive amount of inoculum to establish infection: large pieces of infected root were placed in a layer through which the roots of tea seedlings were allowed to grow. More recently Proffer and others (1988) used extremely large inocula relative to the size of the host: three stem segments 1.2 cm diam x 12-13 cm long were attached to the collar (approx 1 cm diam) of each 1-year-old experimental plant. As mentioned previously, the experiment gave unusually high levels of disease, an outcome which may have been partly due to the high inoculum potential resulting from the inoculation method.

As well as helping to increase inoculum potential, placing inocula close to the host may help to prevent disease escape. Rishbeth (1984), although working in an area and with species in which infection by rhizomorphs is probably the norm, considered it important to place inocula in contact with the host to allow the opportunity for non-rhizomorphic infection by isolates which are poor rhizomorph producers. In studies of species such as *A. tabescens* and *A. fuscipes* that normally infect only through root contacts, inocula are necessarily placed in contact with the host (Dadant 1963a, Plakidas 1941, Rhoads 1938, Rishbeth 1985b, Weaver 1974).

In some experiments with *A. tabescens* and *A. fuscipes* artificial wounds have been made at the point of inoculation (Dadant 1963a, Plakidas 1941, Weaver 1974). Wound inoculation has not commonly been employed with other species though Whitney and others (1989b) reported that such inoculations with *A. ostoyae* on fir roots were more successful than non-wound inoculations.

Rhizomorphs and Measurement of Disease in Inoculation Trials

Assessing virulence in trials has commonly been based on one or more of the following: amount of root infection, amount of mortality, or rapidity of infection or mortality. Such relatively straightforward measurements are, however, often complicated by the need to consider the role of rhizomorphs as extensions of the experimental inoculum.

Serious *Armillaria* diseases occur in several regions of the world where rhizomorph growth is restricted or absent (Dadant 1963a, Dade 1927, Kile 1981, Morrison 1981, Podger and others 1978, Rhoads 1956, Rishbeth 1980). Although non-rhizomorphic infection occurred

commonly in Kile's (1981) inoculation trials with *A. luteobubalina* and Dadant's (1963a) with *A. fuscipes*, it has proved difficult to achieve experimentally with *A. tabescens*, the other economically important species known to infect in this way naturally (Rhoads 1956, Weaver 1974). Non-rhizomorphic infections by temperate species have occasionally been observed in inoculation trials (Rishbeth unpubl., Shaw 1977, Whitney and others 1989b) but some attempts to induce them deliberately have failed (Redfern 1978).

Most *Armillaria* experimentation has involved species in which rhizomorphs have been assumed to be the normal, or only, means of infection; most inoculation experiments have included a final assessment of the presence or absence of rhizomorphs. Among these studies are several reports of isolates which do not produce rhizomorphs readily, or at all, under experimental conditions (Gregory 1985; Mallett and Hiratsuka 1988; Rishbeth 1984; Rykowski 1981c, 1984; van Vloten 1936). Such isolates may eventually produce rhizomorphs given time (Patton and Riker 1959, Gregory unpubl.) or may be induced to do so by altering the method of inoculum production (Redfern 1970, Rishbeth 1968) or inoculum size (Benjamin and Newhook 1984b). Rhizomorph production, and hence disease, may also be strongly influenced by soil conditions (see chapter 4). Consequently, it may be difficult to decide whether lack of rhizomorphs, which is usually associated with lack of infection, reflects genuine field behavior or defective technique.

Interpreting results can be difficult in experiments where inocula in some replications produce rhizomorphs while those in others do not. Gregory (1985) treated such replicates as missing values, and Morrison's (1982b) scoring system also excluded replicates in which no rhizomorph contacted the host. However, some authors have included these data among non-infected categories, accepting the risk that this might distort results of trials with species that are poor rhizomorph producers.

Some of the problems associated with rhizomorph behavior are represented in the data of Mallett and Hiratsuka (1988), who found low disease levels and no rhizomorphs in trials with Canadian isolates of *A. ostoyae*. Since other evidence (discussed below) suggests that this species is a serious pathogen in both North America and Europe, the few infections achieved probably resulted not from low intrinsic pathogenicity but rather from the species' inability to produce rhizomorphs under the experimental conditions. European isolates of the same species have been characterized by Guillaumin and others (1985) and Gregory (1985) as poor producers of rhizomorphs in experiments.

Rhizomorph production may have a bearing on the optimum duration of *Armillaria* inoculation trials, a subject which has been briefly discussed by some authors (Benjamin and Newhook 1984b, Gregory 1985, Mallett and Hiratsuka 1988, Patton and Riker 1959), but which merits further attention. Several studies indicate that certain isolates take longer than others to cause visible, above-ground signs of infection (Gregory 1985, Raabe 1967, Redfern 1975, Rishbeth 1984, Wilbur and others 1972). The three isolates used by Wilbur and others (1972) differed little in virulence assessed simply as the proportion of experimental plants killed at the end of a 3-year trial. They would have been judged to differ markedly from each other, to the extent of one being almost non-virulent, had the final assessment been made after 18 months. Yet, this timespan equals or exceeds that chosen by many workers. In an unpublished trial using methods similar to those of Redfern (1975), Gregory found that 2 years after inoculation *A. mellea* had killed twice as many young conifers as *A. ostoyae*; however, after 3 years the position was reversed and was maintained until the trial ended 5 years after inoculation.

If a relatively slow rate of disease development reflects a relatively poorer ability of rhizomorphs contacting a host to initiate infection, then it may be a legitimate expression of lower virulence as some authors have proposed (Raabe 1967, Rishbeth 1984). If, by contrast, experimental manipulation adversely affects rhizomorph production and subsequently causes slow disease development, then the use of rate in comparative assessments is questionable. Guillaumin and others (1985) have noted that European species differ in the time taken to produce rhizomorphs under experimental conditions. They cite *A. ostoyae* as being especially tardy, an observation that coincides with unpublished data of Gregory and Rishbeth.

Most investigators who have studied pathogenicity in *Armillaria* have measured the amount of disease simply by the proportion of host plants killed or infected during the experiment. Several authors have used lesion size for scoring the severity of non-fatal infections (Gregory 1985, Guillaumin and Pierson 1978, Morrison 1982b, Rishbeth 1982). Assessments of dead or symptomatic plants have nearly always been visual and involved destructive examination. The main exception to the latter is a study by Zollfrank and Hock (1987), who conducted their experiments under aseptic conditions and used immunofluorescence to detect hyphae in seedling tissues.

Field Observation

The century-old descriptions of *Armillaria* disease by Robert Hartig (1874, 1894) reveal the field experience of

a remarkable observer and stand comparison with modern accounts. From this beginning, field observations have been a major source of information about *Armillaria* disease, but they have also fueled much controversy over the role of *Armillaria* as a pathogen. *Armillaria* diseases are probably almost as difficult to observe critically in the field as they are to investigate by experiment. Worthwhile field observations require a comprehensive knowledge of forest pathology and of *Armillaria* biology as well as meticulous site investigation. Regrettably, some studies assume that the situations from which basidiomes have been collected fully circumscribe the ecology and pathogenic behavior of the fungus.

With our present ability to identify separate species of *Armillaria*, field observation has contributed significant information about pathogenicity. Despite Rishbeth's extensive experimental work, an appreciable proportion of our knowledge of pathogenicity in the European species derives from field observations (Gregory 1989; Guillaumin and others 1985; Guillaumin and Berthelay 1981; Korhonen 1978; Rishbeth 1982, 1984, 1985b). Field observations, notably those of Morrison and others (1985a), also constitute a major source of published data on North American species. In New Zealand and Australian studies, inoculation trials have complemented extensive field observations (Kile 1980b, 1981; Kile and Watling 1983; Pearce and others 1986; Podger and others 1978; Shaw and others 1981).

Indirect Methods of Assessing Virulence

Attempts to assess virulence indirectly have had only limited success. The idea of a direct relationship between virulence and host may be traced back to the observations Childs and Zeller (1929) made on what appeared to be a virulent "oak strain" of the pathogen and a non-virulent "fir strain." They were careful to acknowledge the danger of extrapolating their observations to other regions, but the idea of a link between host and virulence has persisted. However, despite having been investigated experimentally a number of times, no such connection has been demonstrated (Guillaumin and Pierson 1978, Raabe 1967, van Vloten 1936).

Possible relationships between virulence and the capacity to produce rhizomorphs have also received considerable attention. The apparent reliance on rhizomorphs for infection was taken by van Vloten (1936) to indicate that isolates which appeared to lack them were de facto non-virulent. Rykowski (1981c, 1984) observed good agreement between infection and rhizomorph production in his numerous experiments and used the relative abundance of rhizomorph growing tips as an index of "infection threat" in his three isolates, all of which

belonged to *A. ostoyae*. Some other studies involving single isolates or several isolates of the same species suggested a positive relationship between infection and rhizomorph production (Azevedo 1970-71, Guillaumin and others 1989a, Shaw 1977), but studies involving several isolates of widely different virulence have generally failed to demonstrate such a relationship (Guillaumin and Pierson 1978, Raabe 1967, Rishbeth 1984). Conversely, some evidence indicates a negative correlation of rhizomorph production to pathogenicity among European species (Gregory 1985, Redfern 1975, Rishbeth 1985b).

Morrison (1972, 1982b) and Redfern (1975) suggested an association between dichotomous branching of rhizomorphs and high virulence. The same authors also noted that highly virulent isolates tended to possess fragile rhizomorphs. We now know that Morrison's (1982b) three branching types represented three different species (Morrison 1989) and that Redfern's (1975) four isolates were also from four species (Gregory 1985). Later studies (Guillaumin and others 1985, Morrison 1989, Rishbeth 1982) have confirmed that branching habit and fragility of rhizomorphs are species characteristics. Morrison's (1989) data, drawn from 15 species, showed that a dichotomous branching habit (fig. 4.1) more often than not accompanied high pathogenicity but the association was not invariable. Three of the eight dichotomously branching species which he tested were of low pathogenicity. It may be unrealistic to seek universal relationships between growth patterns and pathogenicity among species that have evolved to survive in such widely different forest and soil conditions as have the various *Armillaria* species.

A few attempts have been made to assay virulence in *Armillaria* by in vitro characters. The most notable were based on the work of Wargo (1981d) that indicated a link between gallic acid metabolism and virulence in certain North American isolates. Shaw (1984, 1985) tested this hypothesis extensively on a collection of 72 isolates drawn from three continents. He found that although the ability to tolerate gallic acid varied among isolates, differences could not be utilized consistently as markers for virulence. Rishbeth (1986) reached a similar conclusion.

Differences in Pathogenicity and Virulence

Although taxonomists have for decades postulated the existence of several morphological species of *Armillaria* (see chapter 1), the recognition by pathologists of distinct pathogens has been comparatively recent. Two major exceptions were provided by *A. tabescens*,

which was accepted as a pathogen in its own right in the southern United States in the 1940's, and *A. fuscipes*, which Dadant (1963a) demonstrated to be a root pathogen of woody plants in Madagascar. Otherwise, before the late 1970's forest pathologists generally referred attacks of *Armillaria* disease to a single but variable taxon with worldwide distribution, "*Armillaria mellea*."

Some older data on the pathogenicity of "*Armillaria mellea*" have been reinterpreted relative to current taxa, but much information from before 1970 is of limited value. Modern studies of pathogenicity and virulence have concentrated largely upon North American, European, and Australasian isolates. Outside these regions, pathogenic species of *Armillaria* undoubtedly exist (see chapter 9), but little is known about the variation among them.

European and North American Species

Although forming a rather artificial grouping, these species are considered together because at least three, including the major pathogens *A. mellea* and *A. ostoyae*, appear to be common to both continents.

Evidence from inoculation trials identifies *A. mellea* as probably the most pathogenic species in this group. In Europe, isolates of this species have not only consistently been ranked highest in comparative studies but have also been demonstrated to cause disease in genera normally regarded as highly resistant to *Armillaria* (Davidson and Rishbeth 1988; Gregory 1985; Guillaumin and Pierson 1978*; Morrison 1982b*; Redfern 1975*; Rishbeth 1982, 1984). Three Canadian trials have included European isolates of *A. mellea* alongside North American isolates of other species, and in all cases the former have proved the most virulent (Mallett and Hiratsuka 1988; Morrison 1989, and pers. comm.; Mugala and others 1989). However, the results of inoculation experiments done by Guillaumin and Lung (1985) suggest that *A. mellea* may be less pathogenic than *A. ostoyae* to some conifers, an outcome which the authors interpreted as evidence of host specialization.

Field observations in Europe indicate that *A. mellea* is the most pathogenic species on ornamental trees, orchard crops, and vines (Guillaumin and Berthelay 1981; Guillaumin and others 1985; Intini 1988; Rishbeth 1982, 1985a). Even though it often kills ornamental conifers, and some isolates are extremely virulent toward young conifers in experiments, it is not widely associated with disease in forest or plantation conifers. In the United

*Isolates in Redfern (1975) were identified by Gregory (1985); those in Guillaumin and Pierson (1978) were identified by Guillaumin and Berthelay; those in Shaw (1977) were identified by Shaw (1984) and those in Morrison (1982b) were identified by Morrison (1989).

States, Proffer and others (1987, 1988) found that *A. mellea* was associated with root disease of cherry in Michigan, but few other observations on North American isolates involve this species.

In inoculation trials, North American and European isolates of *A. ostoyae* have generally been moderately or highly virulent towards young conifers (Gregory 1985; Guillaumin and Lung 1985; Morrison 1982b, 1989; Redfern 1975; Rishbeth 1982, 1984, 1985b; Shaw 1977; Siepmann and Leibiger 1989). Under experimental conditions, the species appears to be only weakly pathogenic to European forest hardwoods (Lung-Escarmant and Taris 1989, Rishbeth 1984). Rishbeth's (1984) data suggest that *A. ostoyae* could be classed with *A. gallica* as virtually non-pathogenic to common ash and silver birch although the isolates of *A. ostoyae* used were highly virulent to Scots pine in the same trial. Proffer and others (1988) found Michigan isolates of *A. ostoyae* to be highly virulent to *Prunus* species, but interpreting their results requires caution because of the equally high disease levels achieved with *A. gallica* isolates in the same experiments. Possible reasons for this have been discussed earlier in this chapter.

Isolates of *A. ostoyae* showing low virulence towards conifers have been reported in Europe (Rishbeth 1984), and recently, Mallett and Hiratsuka (1988) demonstrated apparently uniform low virulence toward young lodgepole pines in a range of Canadian isolates. As suggested earlier, such results may reflect the poor ability of some isolates to produce rhizomorphs under experimental conditions rather than innate low virulence. Indeed, *A. ostoyae* may be consistently under-rated in inoculation studies for this reason.

Field observations in North America (Bloomberg and Morrison 1989, Dumas 1988, Harrington and others 1989, Mallett and Hiratsuka 1988, Morrison and others 1985a), Fenno-Scandia (Korhonen 1978, Piri and others 1990), and Europe (Gregory 1989, Guillaumin and Berthelay 1981, Guillaumin and others 1985, Intini 1988, Rishbeth 1985a, Siepmann 1985) indicate that *A. ostoyae* is a major forest pathogen of conifers in those regions. Several of these accounts show the species can kill trees of all ages and can also cause butt rot in older crops. So consistently has *A. ostoyae* been associated with disease in conifers that it is commonly assumed to be the probable pathogen whenever serious *Armillaria* disease is encountered in North American or European coniferous forests (Filip 1989a, Hadfield and others 1986, Hansen and Goheen 1989, Rizzo and Harrington 1988a, Whitney 1988b).

Despite the low pathogenicity towards hardwoods indicated by inoculation experiments, field observations suggest that *A. ostoyae* is capable of attacking

broadleaved trees and shrubs growing within diseased conifer stands (Guillaumin and others 1985, Morrison and others 1985a, Rishbeth 1985a). Harrington and others (1989) recorded it as a cause of death of birch and maple in the northeastern United States, and the observations made in Canada by Dumas (1988) suggest that it may have a rather wide host range among hardwoods there, at least as a secondary pathogen.

Armillaria gallica has been widely categorized as a weak pathogen by both field observations and inoculations in Europe and North America (Gregory 1985, 1989; Guillaumin and Berthelay 1981; Guillaumin and Pierson 1978; Guillaumin and others 1985; Morrison 1989; Morrison and others 1985a; Redfern 1975; Rishbeth 1982, 1984; Shaw 1977, 1984; Siepmann and Leibiger 1989). Some isolates have been designated as virtually non-virulent (Rishbeth 1982, Shaw 1984), yet in few trials has this species completely failed to cause disease. In some cases (Guillaumin and Pierson 1978, Proffer and others 1988), it has caused appreciable damage, albeit to highly susceptible species. As already discussed, the level of damage achieved in trials with young, and possibly stressed, experimental plants may be artificially high. However, since newly planted crop or ornamental trees are also often young and stressed, it might therefore be unwise to dismiss comparatively weak pathogens such as *A. gallica* as harmless. Moreover, the ability of *A. gallica* to act as a secondary agent of mortality in large trees and to cause root- and butt-rot in live trees (Gregory 1985, Rishbeth 1982) implies a far from negligible capacity to cause disease. These remarks apply to most of the other species categorized below as weak pathogens.

Armillaria cepistipes is regarded in Europe as an analogue of *A. gallica*: a weak pathogen virtually indistinguishable from *A. gallica* in behavior and appearance (Guillaumin and others 1985). Few inoculation trials have been reported for this species, but those of Redfern (1975) and Morrison (1989) both indicated low virulence in the isolates tested. Rishbeth has unpublished data from the trials reported in 1985b, table 3, that also demonstrate low virulence. The species is nevertheless associated with butt rot of conifers in Finland and Scotland (Gregory 1989, Korhonen 1978, Piri and others 1990).

Of the six North American biological species (NABS) not clearly identified with European species (*A. gemina*, *A. calvescens*, *A. sinapina*, NABS IX, NABS X, and NABS XI), *A. sinapina* (NABS V) has probably received most attention because it is relatively common in some important forest areas (Mallett and Hiratsuka 1988, Morrison and others 1985a, Shaw and Loopstra 1988). The inoculation experiments with young trees in containers carried out by Morrison (1989), Mugala and

others (1989), and Shaw and Loopstra (1988) suggest that the species is of low pathogenicity towards some North American conifers. However, in another trial, Mallett and Hiratsuka (1988) found more infection caused in potted lodgepole pine by Canadian isolates of *A. sinapina* than by *A. ostoyae*. Although, as noted above, the latter may have been seriously underestimated in this experiment, the data for *A. sinapina* are nonetheless anomalous, the more so as Mugala and others (1989), using similar methods, reported low virulence towards the same host by one of the same isolates. Field observations in Canada support the view that *A. sinapina* is a weak pathogen (Dumas 1988, Morrison and others 1985a).

NABS IX also appears to have limited pathogenicity towards young conifers according to field observations and inoculation trials in British Columbia and Alaska (Morrison and others 1985a, Morrison 1989, Shaw and Loopstra 1988). Shaw and Loopstra (1988) found that haploid isolates of this species and *A. sinapina* caused significantly more disease than the parent isolates.

The observations of Morrison and others (1985a) in British Columbia placed the other northwestern species, NABS XI, in the same category as *A. gallica*, *A. sinapina*, and NABS IX. All are weak pathogens characteristic of suppressed or overmature hardwoods. The results of Morrison's (1989) subsequent inoculation trial with young Douglas-fir in pots supported this view since all four species received the same very low rating.

Armillaria gemina (NABS II) and *A. calvescens* (NABS III) were also included in Morrison's (1989) trial. Both were accorded the same low rating as NABS IX, NABS XI, *A. sinapina*, and *A. gallica*. Despite this, field observations on *A. calvescens* by Proffer and others (1987) in Michigan and by Harrington and others (1989) in New Hampshire associate it with root rot and mortality of hardwoods. In the case of *A. gemina*, Bérubé and Dessureault (1989) have stated that it is "identical to *A. ostoyae* in terms of . . . pathogenicity," but this view is based on extremely limited field observations. Little is known about the pathogenicity of NABS X, although McDonald (1990) suggests, again from limited observations, that it may be moderately pathogenic.

The northern European species *A. borealis*, which has not been recorded in North America, is generally regarded as a rather weak pathogen (Guillaumin and others 1985, Korhonen 1978), though observations from Britain suggest that some genotypes might be virulent to young conifers (Gregory 1989). Korhonen (1978) identified *A. borealis* as an important cause of butt rot of Norway spruce in Finland, and it has been associated with similar damage in Germany and Britain (Gregory

1989, Siepmann 1985). Only two inoculation trials have been reported. Both utilized young potted conifers; and both suggested that *A. borealis* is a rather weak pathogen, intermediate between *A. mellea* and *A. ostoyae* on one hand and *A. gallica* and *A. cepistipes* on the other (Morrison 1989, Siepmann and Leibiger 1989).

Although *A. tabescens* has been cited as causing root disease in trees in several parts of the world, considerable doubt now exists that a single species is involved (see chapter 1). Most information is available from the southern United States, where it is known as a serious pathogen of ornamental trees and commercial crops (Rhoads 1956, Sinclair and others 1987). The fungus can attack a wide range of woody species in a variety of genera but, according to Rhoads (1956), exotics are much more susceptible than native trees and shrubs. Rhoads (1956) also reported that damage caused by *A. tabescens* was particularly prevalent on drought-prone sites, and Weaver (1974) suggested that disease in peach only followed infection of previously killed or injured roots. Other reports associate *A. tabescens* with disease in stressed trees or trees primarily attacked by other agents (Filer and McCracken 1969, Ross and Marx 1972, Sinclair and others 1987).

A fungus referred to as *A. tabescens* has also been recorded in southern Europe as a root pathogen on several hosts including citrus on Corsica (Laville and Vogel 1984), eucalypts in southwestern France (Lung-Escarmant and others 1985a), and cork oak in Portugal (Azevedo 1976). Further north, European isolates of *A. tabescens* appear to be non-virulent in the sense of causing root mortality, though field observations have linked the species with decay of live trees in Britain (Rishbeth 1984, 1985b). The apparently southern distribution of diseases attributed to *A. tabescens* in both Europe and the United States is noteworthy because observations in China (Chang and others 1982) also associate severe root infection by *A. tabescens* with high soil temperature.

Australasian Species

Three Australasian species are regarded as serious pathogens on the evidence of field observation and inoculation trials: *A. luteobubalina*, *A. novae-zelandiae*, and *A. limonea*. Isolates of all three were represented in Morrison's (1989) trial which tested a range of European, North American, and Australasian species against 2-year-old Douglas-fir seedlings in containers. His results suggested that the three Australasian pathogens may be ranked with *A. mellea* and *A. ostoyae*. However, the amounts of disease recorded in most Australasian trials have been low by comparison to European or North American results with *A. mellea* and *A. ostoyae*. The contrast is particularly noteworthy in

similar tests on radiata pine conducted by Shaw (1977) in the United States with *A. gallica* and *A. ostoyae* and by Shaw and others (1980, 1981) in New Zealand with *A. novae-zelandiae* and *A. limonea*).

Field observations in New Zealand by MacKenzie and Shaw (1977) and Shaw and Calderon (1977) attributed disease in radiata pine crops to two native *Armillaria* species, *A. novae-zelandiae* and *A. limonea*, with the former appearing to be the more serious pathogen. Inoculation trials with young radiata pine in containers (Shaw and others 1980, 1981) demonstrated that both species were moderately pathogenic although some isolates of each had low virulence. Benjamin and Newhook (1984b) undertook trials with the same two species and found them highly pathogenic toward radiata pine, but in tests with eucalypts, *A. limonea* seemed to be less pathogenic than *A. novae-zelandiae*.

Armillaria novae-zelandiae also occurs in Australia where Kile and Watling (1983) recorded it as a secondary pathogen of native trees and a frequent cause of decay in myrtle beech. More recently, it has been cited by Kile and Watling (1988) as causing localized losses in young crops of exotic conifers, in which it is linked with *A. fumosa* and *A. pallidula*. Little else is known about either of these species though an isolate of *A. fumosa* was included in Morrison's (1989) trial in which it proved virtually non-virulent.

The chief Australian pathogen is undoubtedly *A. luteobubalina*. Field observations (Kile 1981, Kile and others 1983, Pearce and others 1986, Podger and others 1978, Shearer and Tippet 1988) have repeatedly demonstrated that it is a major primary pathogen in native sclerophyll forests where it kills eucalypts and a wide range of understory trees and shrubs. Infection can occur on eucalypts of all ages, resulting in crown dieback or mortality of large overstory trees as well as serious losses among seedlings and saplings. The fungus also attacks a wide range of species in vineyards, orchards, and ornamental plantings (Kile and Watling 1988).

Armillaria hinnulea by contrast was found to be weakly pathogenic in inoculation experiments with both native species and North American conifers (Kile 1980b, Morrison 1989). Morrison's (1989) data indicate that this species is similar to the European *A. borealis* in its ability to infect young Douglas-fir in containers. Field observations have characterized *A. hinnulea* as a weak pathogen capable of causing localized root lesions and decay in resistant hosts. It is nevertheless an effective secondary pathogen, and in this capacity, it is of some economic importance in Tasmania through association with "regrowth dieback," a decline of eucalypts of

which the primary cause is unknown (Kile 1980b, Kile and Watling 1983).

Non-Australasian Tropical and Subtropical Species

Dadant (1963a) demonstrated experimentally that the morphological species he knew as *A. elegans* was pathogenic to field-grown albizia sp. His detailed observations and numerous isolations leave little doubt that the fungus he studied is a serious pathogen of coffee bushes and shade trees in Madagascar. Blaha (1978) associated the same fungus with damage to a similar range of hosts in Cameroon. The fungus is now known to occur widely in Africa and to be conspecific with *A. fuscipes* (see chapter 1), which was described by Petch (1923) as a root pathogen of acacia and probably also of tea bushes in Sri Lanka.

Most of the numerous accounts of *Armillaria* diseases in tropical and subtropical crops (see chapter 9) cannot now be validly attributed to morphological or biological species. However, the recent work by Mohammed and others (1989) with African isolates suggests that other pathogenic species in addition to *A. fuscipes* occur on that continent. Ironically, one of these appears to be at least partially interfertile with *A. mellea*—the name associated by default with disease in Africa since the early years of this century.

Conclusions

The genus *Armillaria* contains several virulent pathogens and other species that have evolved as successful secondary or facultative pathogens. Failure to appreciate this variation within the genus probably accounts for much of the controversy that has arisen in the past over the pathogenic status of *Armillaria*. Without doubt some species are primary pathogens, though the amount of disease caused by even the most pathogenic taxa may be conditional upon the nature of the host and the environment of the fungus. Most species appear to have a wide host range, but some species are apparently adapted to particular groups of hosts or site conditions or both. There is strong evidence that virulence differs among isolates of some species.

Experimentation with *Armillaria* poses formidable problems, and the interpretation of data from experiments and field observations is rarely straightforward. Nevertheless, our understanding has advanced remarkably rapidly in the past 20 years, though many aspects of pathogenicity merit further investigation. Despite the advances, relatively little is known about several North American biological species and even less about tropical and subtropical species.

Host Stress and Susceptibility

Philip M. Wargo and Thomas C. Harrington

Armillaria root disease has historically been considered a disease of weakened trees. Early observers indicated that *Armillaria* was secondary to some other factor that predisposed trees to attack (Day 1927a, 1928, 1929; Falck 1918, 1923; Müller 1921; Nechleba 1915, 1927; Thomas 1934). Although not always the case, predisposition is considered common with *Armillaria* root disease, and seems to be more important in this disease than in the other woody root diseases of forest, shade, and orchard trees.

As with all diseases, susceptibility to *Armillaria* root disease depends on interactions among host, pathogen, and the environment. The importance of predisposing stresses and their impact on host vigor (the environmental component) must be considered in the context of the host and the pathogen. *Armillaria* has an extremely broad host range (Raabe 1962a), but these hosts vary in their susceptibility. Furthermore, many species of *Armillaria* are now recognized and these vary greatly in their pathogenicity (see chapter 6). Some are primary pathogens capable of killing vigorous hosts while others colonize only severely stressed individuals.

Stresses generally predispose trees to *Armillaria* root disease by reducing host vigor and, thus, compromising host defenses. Host defense mechanisms are addressed in chapters 4 and 5, but a brief review will set the stage for our discussion of stress and predisposition. Chronic and acute stresses and how they might affect resistance are covered in general, and specific examples of abiotic and biotic stress agents known to predispose trees to *Armillaria* are given. Lastly, we discuss forest management of *Armillaria* root disease relative to stress-induced susceptibility.

Stress Concepts and Host-Pathogen Interaction

Variation Among *Armillaria* Species, Host, and Site

Confusion about *Armillaria* taxonomy has hampered our understanding of stress effects on disease development. Unfortunately, very little research on stress-induced susceptibility has been conducted with known species of *Armillaria*. Where species of *Armillaria* have been identified, evidence suggests that root disease caused by *A. mellea*, *A. ostoyae*, or *A. gallica* is more likely to occur in a stressed host (Davidson and Rishbeth 1988).

Obviously, variation in pathogenicity among the *Armillaria* species (see chapter 6) has an important bearing on the requirement for a predisposing stress in disease development. *Armillaria gallica* only attacks stressed trees (Davidson and Rishbeth 1988) whereas *A. mellea* and *A. ostoyae* can infect and kill apparently vigorous trees. Stress may also broaden the host range of some *Armillaria* species. For example, *A. ostoyae* attacks primarily conifers but will also attack oaks when they are stressed (Davidson and Rishbeth 1988).

Predisposing stresses may be more important for disease development in relatively resistant species than in the more susceptible species. In general, hardwoods are considered more resistant to *Armillaria* root disease than coniferous species in northern temperate forests (Redfern 1978, Rishbeth 1972a). As discussed later, predisposing factors have been more often noted in *Armillaria* root disease on hardwoods than on conifers. However, *Armillaria* may be equally aggressive on healthy hardwoods, and this observation may reflect

the limited distribution of *A. mellea*, the species most capable of colonizing apparently healthy hardwoods (Davidson and Rishbeth 1988, Rishbeth 1982). Also, research on root and butt rots in hardwoods has been limited, and the disease may be more prevalent on hardwoods than commonly realized (Nordin 1954, Shigo and Tippet 1981).

Very limited information is available on resistance among hardwood species, but work on rootstocks of horticultural species shows that resistance varies both among and within species. Thomas and others (1948) reported that pear and walnut were quite resistant to *Armillaria*, but apricot and prune were susceptible. Variation in root stock resistance among several *Prunus* species was also reported in France (Guillaumin and Pierson 1983). Both studies demonstrated that peach and apricot root stocks were more susceptible to *Armillaria* than plum root stocks. Recent work by Guillaumin and others (1989b) verified that this relationship exists for *A. mellea sensu stricto*. The resistance of plum species was a dominant trait, and resistance to infection and colonization was maintained in some plum x peach hybrids.

Armillaria root disease occurs on many coniferous species (Raabe 1962a), but resistance varies considerably among and within species. In an English forest where Scots pine and Norway spruce were growing together, large patches of pine were killed while spruce were unaffected (Rishbeth 1972a). Inoculation studies on small trees, comparing resistance between conifers and hardwoods, showed that large differences existed among tree species in the percent of trees infected by *Armillaria*, and in the ratio of killed trees to surviving-infected trees; the hardwood species were generally the most resistant (Redfern 1978). Morquer and Touvet (1972b) also noted variation in resistance among conifer species, but no species tested was immune to infection.

Differences in resistance clearly occur within and among host species, but much of this observed difference may be related more to tree vigor than to genetic resistance. The importance of tree vigor in *Armillaria* root disease and the interplay of vigor and resistance make ranking of species susceptibility difficult, even with inoculation data (see chapter 6). Likewise, unless clonal material is available, identifying the importance of stresses and tree vigor is difficult.

Site factors and host adaptation play an important role in host vigor and susceptibility to *Armillaria* root disease. McDonald and others (1987a) found that the incidence of pathogenic *Armillaria* was low in habitat series

of high productivity, unless the site was disturbed. In habitat series of low productivity, *Armillaria* was pathogenic in both disturbed and pristine sites. Disturbance was associated with increased disease incidence, but the association was weaker in highly productive sites where adaptive tolerances of the tree species were not exceeded. They suggested that *Armillaria* root disease was a problem on conifers in sites affected by human activities (including fire suppression), insects, or diseases, and in pristine sites where tree species were not adapted physiologically to their environment.

While little experimental work has been done to test this hypothesis, observations on where *Armillaria* is or has been a problem in forest stands tend to support it. For example, in the Northwestern United States *Armillaria* problems often occur in off-site plantations (Hadfield and others 1986, U.S. Dept. Agric. 1983) or transition forests that have been perpetuated by fire and disturbed recently by logging activity and fire control (Shaw and others 1976a). Problems with exotic species can also be related to maladaptation. Although these species may grow very well in new regions, they may not be well adapted to the climatic extremes in their new habitat. Consider, for example, radiata pine in high rainfall areas in New Zealand (Hawkins and Sweet 1989a,b). The factors important to site adaptation and tolerance of climatic extremes, including such physiological processes and conditions as net photosynthesis, cold and drought tolerance, and genetic variability, are also related to resistance to *Armillaria* root disease.

Host Vigor and Predisposition

The term "vigor" has been used to describe the overall robustness of a tree as indicated by its relative growth and absence of signs and symptoms of disease. Vigor is determined by a tree's physiological performance within a particular environment, and this performance depends upon the tree's genetic capacity. Genetic variation gives a range of physiological performances and therefore a range of physiological conditions or tree vigors under a given set of environmental conditions. Crown position (dominant, intermediate, or suppressed) and crown condition (good, fair, or poor) are commonly used to classify tree vigor. These are good indices of a tree's past relative growth and general vigor. However, they indicate little about a tree's current health and its vulnerability to the effects of stress (Wargo 1978a,b,c). When stressed by defoliation, for example, trees in all of the above vigor categories may be attacked and killed by *Armillaria* (Wargo 1977), indi-

cating that within these general vigor categories there are gradations of tree health. Herein, host vigor refers to the tree's current health and vulnerability.

Yarwood (1976) defines predisposition as "... the tendency of treatments and conditions acting before inoculation or before the introduction of the incitant, to affect susceptibility to biotic and abiotic pathogens." In the strict sense of this definition, trees are not always predisposed to infection by *Armillaria* since the pathogen may have already infected the roots prior to the stress. Many observations, especially in the *Armillaria*-hardwood relationship, suggest that for some combinations of hosts and *Armillaria* species the fungus rarely infects and colonizes an unstressed tree despite epiphytic pathogen growth on root surfaces (see chapter 8). Yarwood's broader definition of predisposition also includes changes that induce greater resistance to disease; however, only examples of increased susceptibility are emphasized in this chapter.

Predisposition to disease may play a much larger role in pathogenesis of forest-tree species than in other plant types because of their longevity. During the lifespan of a tree, it may be exposed to numerous stress-inducing episodes ranging from mild to acute and from short-term to chronic. Also, stresses that were inconsequential during a tree's early years can have devastating effects on the tree later. As trees increase in size and completely occupy their sites, their ability to maintain adequate moisture, nutrients, and energy levels approaches the physical limitations of the root and shoot systems; stresses can then cause considerably more damage.

Resistance to pathogenic organisms is the rule rather than the exception in forest trees. "If this were not so, they [trees] would have ceased to exist," (Shain 1968); or at least they would not live as long as they do. Although all trees have some capacity to resist infection, this resistance requires substantial energy. This metabolic energy is necessary to maintain or synthesize structural or chemical defenses that influence growth of pathogens at the surface of the plant or internally (Wood 1967). Production of physical and chemical barriers depletes the host's energy reserves, and trees of less than optimal vigor may not have the energy reserves required to resist infection and are therefore predisposed to disease. Conversely, host species with little genetic resistance will succumb if the pathogen is present, regardless of their energy reserves.

Stresses and Resistance to *Armillaria*

The term "stress" has been used to describe any environmental factor that can have potentially unfavorable

influences on living organisms. Levitt (1972) defines "biological stress" as "any environmental factor capable of inducing a potentially injurious strain in living organisms" and "biological strain" as any change produced by the stress. The strain may be physical, such as the reduction of water flow through the transpiration stream in trees, or it may be chemical, such as a shift in carbohydrate metabolism.

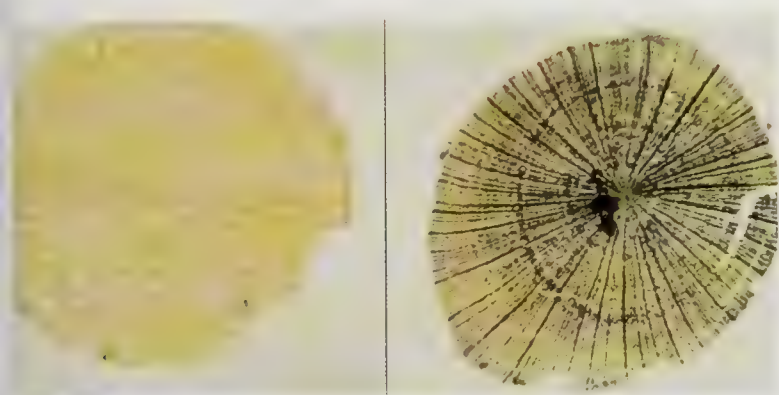
Chronic and acute stresses may disturb plants by altering resource allocation or by interfering with sink-source relationships (Waring and Patrick 1975). Stresses may interfere with the resistance response by reducing the energy reserves available for reaction (McLaughlin and Shriner 1980). Acute stresses may also temporarily impede metabolism at the infection site, and thus compromise the resistance response. The effects of a particular stress depend on severity, duration, season, frequency of occurrence, and the condition of the tree when it is stressed (Wargo 1978a,b).

Starch content has been used as an indicator of physiological performance and the effects of stress (Wargo 1978c). The susceptibility of stressed trees that are low or depleted in starch content probably relates, in part, to the reduced energy available for defense reactions (McLaughlin and Shriner 1980). For example, many oak trees are colonized by *Armillaria* after defoliation by the gypsy moth, but not all trees are infected, and not all infected trees are colonized to the same extent (Wargo 1977). Mortality of oak and sugar maple after defoliation was related to carbohydrate production and storage (Wargo 1981b,c,e; Wargo and Houston 1974). Trees with low or depleted starch when defoliation occurred were more likely to be colonized by *Armillaria* and to die after stress from defoliation (fig. 7.1). Starch content at the time of stress was related to how long a tree survived and how many defoliations it could tolerate.

Barriers and Energy Reserves

Preformed physical barriers such as outer bark play an important role in protecting roots from invasion by pathogens (see chapters 4 and 5). Outer bark may offer less protection from *Armillaria* than from those root-rotting fungi that cannot penetrate without wounds. Existing evidence does not suggest that predisposing stresses enhance susceptibility by allowing penetration through intact outer bark. However, some stress agents may cause bark injury and provide infection courts for *Armillaria*. Wind-induced root movements and breakage (Harrington 1986, Hintikka 1972, Rizzo and Harrington 1988b), rock abrasions (Stone 1977), and insect feeding provide infection courts for *Armillaria* and other root pathogens (Redmond 1957, Whitney

A



B

FIGURE 7.1 — *Armillaria* and energy reserves in roots of sugar maple. A: Sections of roots from defoliated (left) and non-defoliated (right) trees inoculated with *A. gallica* and incubated for four weeks; B: Starch reserves in roots from defoliated (left) and nondefoliated (right) trees in the fall after defoliation. Starch grains have been stained with I²KI and appear purple-black in the tissue. (P. Wargo)

1961). Wounding and root breakage also stress trees since the tree must expend energy to close the wound, prevent infection, and replace damaged roots.

Wounds may not be so important in removing the barrier of the dead outer bark as they are in removing the living, responsive, inner bark. Once the outer bark is penetrated, the pathogen encounters living tissues where physiological factors, such as lytic enzymes or toxic secondary metabolites, may limit hyphal penetration of the inner bark.

The limitation of *Armillaria* hyphae developing within healthy host plant tissues has been described for the mycotrophic association between the fungus and achlorophyllous orchids (Hamada 1940, Kusano 1911, see chapter 8). In this relationship, lysis of the hyphae and reinfection by the fungus occur seasonally. The mechanism of hyphal lysis is unknown, but it could

result from digestion by host enzymes. Chitinase and B-1,3-glucanase, enzymes that can dissolve the hyphal wall of *Armillaria*, are present in the inner bark and sap of forest tree species (Wargo 1975), and they constitute a potential mechanism to limit the growth of *Armillaria calvelescens* hyphae in resistant bark tissue (Wargo 1975, 1976, and unpubl.). The activities of these enzymes are reduced by stress from defoliation (Wargo 1976).

An important component of the resistant reaction of the inner bark is the formation of wound periderms (Biggs and others 1984, Rykowski 1975, Thomas 1934). Some general observations indicate that stressed trees cannot produce periderms rapidly or fail to form wound periderms in response to *Armillaria* (Rykowski 1975). Even if they are formed, under some circumstances *Armillaria* has the ability to penetrate such suberized periderms (Rykowski 1975), probably by enzymatic degradation (Swift 1965, Zimmermann and Seemüller 1984).

Conversion of extant energy reserves into secondary compounds in response to wounding or invasion of inner bark or sapwood may benefit the host by forming compounds that are directly toxic to the pathogen, that are unavailable for pathogen metabolism, or that protect more complex carbohydrates from fungal extracellular enzymes (Worrall and Harrington 1988b). Gums, resins, phenolic compounds, and other metabolites may be produced in higher concentrations in response to wounding or invasion by pathogens than in unaltered sapwood (Hepting and Blaisdell 1936, Shain 1967).

Oleoresins in the inner bark and sapwood of conifers are potentially inhibitory to the fungus and are secreted in response to infection and colonization by *Armillaria*. Volatile components of oleoresin from Scots pine reduced the growth of *Armillaria* on agar by half (Rishbeth 1972a), and fewer rhizomorphs of *A. ostoyae* developed from resinous rootwood of Corsican pine than from non-resinous rootwood (Rishbeth 1985b). Roots of stressed conifers do not produce as much resin as healthy trees, and root tissues are colonized by fungi more rapidly than are roots of unstressed trees (Gibbs 1967, 1968; James and others 1980a,b; Rykowski 1975).

In spite of the emphasis on the role of the fungus as a phloem colonizer, *Armillaria* is capable of colonizing the inner wood of roots and stems without killing phloem tissues. This typical root- and butt-rot colonization may occur in relatively vigorous trees capable of resisting phloem colonization, and may proceed for decades without host mortality (Shigo and Tippet 1981, Tippet and Shigo 1981).

Two general sapwood responses are known (see chapter 5). First, sapwood tissues may be converted to non-living, reaction zone tissues that resist pathogen coloni-

zation (Shain 1967). Inhibitory, secondary compounds similar to those in the inner bark are also found in the reaction-zone tissues of the sapwood. As discussed in connection with the inner bark, these compounds require substantial energy reserves, and in stressed trees may not be produced in sufficient quantity or soon enough to stop *Armillaria* colonization.

Second, whether or not the pathogen becomes established in the reaction zone, another impediment to pathogen development, the barrier zone, may be formed. The cambium may respond by producing a unique layer of xylem that resists penetration by the pathogen and tends to restrict it to those growth rings of xylem formed prior to injury (Hepting and Blaisdell 1936, Shigo and Larson 1969). Barrier zones of this sort, formed in response to infection and colonization by *Armillaria*, have been observed in roots of both conifers and hardwoods (Shigo and Tippet 1981, Tippet and Shigo 1981).

Although evidence is limited, sapwood and cambium of less vigorous trees may form less inhibitory reaction zones and weaker barrier zones than the sapwood and cambium of healthy trees (Armstrong and others 1981, Shearer and Tippet 1988, Shigo and Hillis 1973). In such cases, *Armillaria* may be slowed but not stopped from developing in the sapwood, and continued development reduces the amount of sapwood available for water transport, increases the energy expended in resistance responses, and may allow penetration from the sapwood into the cambium and inner bark.

Pathogen Nutrition

Stress also affects resistance indirectly by nutritionally enhancing *Armillaria* growth. Predisposition of defoliated sugar maple to *Armillaria* occurs in part through changes in the carbohydrate and amino nitrogen compounds induced by defoliation (Wargo 1972).

Severe defoliation triggers hydrolysis of starch and results in large increases in reducing sugars in the cambial zone and neighboring tissues (Parker 1970, Parker and Houston 1971, Wargo 1972, Wargo and others 1972). Qualitative and quantitative changes in amino nitrogen also occur (Parker and Patton 1975, Wargo 1972) and, combined with increases in glucose, significantly stimulate the growth of *Armillaria calvescens* in vitro (Wargo 1972, 1981a, and unpubl.) (fig. 7.2). Hydrolysis of starch to glucose would certainly be more beneficial (nutritionally) to *Armillaria* than would conversion of starch to secondary metabolites, as would occur in the production of reaction zone tissues in healthy trees.

Stresses, such as excess soil moisture and defoliation, may also increase the ethanol in root tissues (Wargo unpubl.). Ethanol is a potent growth stimulant for *Armillaria* (Weinhold 1963) and its presence in root tissue could affect susceptibility to the fungus. The host may directly produce ethanol in response to stress (Coutts and Armstrong 1976, Crawford and Baines 1977); ethanol may be produced by associated microorganisms and promote the growth of *Armillaria* (Pentland 1967); or under anaerobic conditions, *Armillaria* may produce its own ethanol (Tarry 1969).

Chemical changes in roots of stressed trees apparently allow the fungus to metabolize phenols and probably other compounds that would normally inhibit it (Wargo 1980a, 1981d, 1983b, 1984a,b). Glucose, ethanol, and nitrogen levels and nitrogen source affect the ability of the fungus to oxidize phenols in vitro. Oxidation and polymerization of phenols by *Armillaria* can remove those that are inhibitory or that precipitate extracellular fungal enzymes. Also, phenol metabolism affects melanin formation by *Armillaria* (Bell and Wheeler 1986, Malama and others 1975, Worrall and others 1986) and could provide rhizomorphs and penetrating hyphae greater protection against enzymatic lysis from host-produced enzymes (Bloomfield and Alexander 1967). All of these host-pathogen biochemical interactions are discussed more fully in chapter 3.

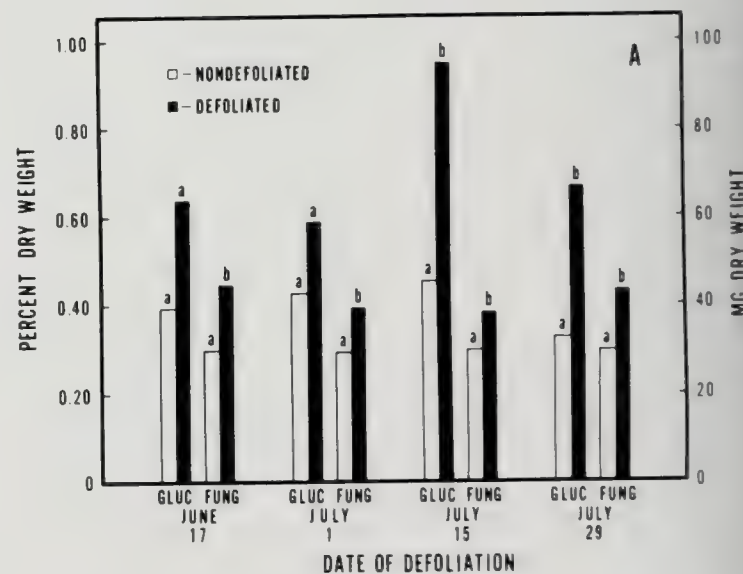


FIGURE 7.2 — Reducing sugar concentrations (% dry wt) in extracts from roots of defoliated and nondefoliated sugar maple, and fungal dry weight of *A. calvescens* after 3 weeks' growth on the extracts. Unlike letters above the bars indicate a significant difference at $P=0.01$. (Modified from Wargo 1972)

Stress Agents and Armillaria Root Disease

General

Trees are exposed to stress throughout their lives. Stresses such as drought, waterlogging, frost damage, some pollution events, insect defoliation, other tree diseases (especially foliar diseases), and short-term coppice cutting may be considered acute (short duration, high intensity). Other stresses may be considered chronic in that the tree may be exposed over its life time to low but relatively constant levels of the stress. Air pollutants, soil nutrient deficiencies, and long-term moisture deficiencies are examples of chronic stress. Shade-intolerant trees in forest understory can also be considered chronically stressed from reduced light.

Acute stresses may affect the metabolism of the entire tree, and *Armillaria* may rapidly colonize the entire root system or the root collar region of such trees and kill them quickly. Colonization of the roots of defoliated oak and sugar maple exemplifies this relationship (Wargo 1977, Wargo and Houston 1974). When acute stresses affect only a portion of the tree, *Armillaria* invasion may be partial and sometimes progressive, causing the tree to die slowly over several years. The relationship of *Armillaria* and beech bark disease demonstrates this interaction. *Armillaria* usually colonizes only those roots of American beech that are associated with the portion of the stem killed by *Nectria coccinea* var. *faginata* Lohman, Watson and Ayers, a canker-causing fungus (Wargo 1983a).

The timing of the stress event is also very important (Wargo 1978b). Stresses that occur early in the growing season and then abate have less of an effect than mid-season stresses because the trees have more of the growing season in which to recover. Likewise, stresses occurring late in the growing season may cause less harm because most of the growth and energy production by the tree has already occurred. The effects of any stress, no matter when it occurs, ultimately depend on its duration within and across growing seasons.

Stresses may also interact. Defoliation by phytophagous insects, especially those associated with oaks, have historically been linked to drought (Falck 1918, 1923; Houston 1981a,b, 1984; Nechleba 1915). These two stress factors working in concert affect tree health, resulting in widespread mortality, much of it associated with *Armillaria*. Defoliation can also exacerbate *Armillaria* root disease on beech affected by beech bark disease. On defoliated trees, *Armillaria* spreads from existing lesions on roots associated with the stem canker into adjacent roots and root collar tissues, resulting

occasionally in rapid mortality (Houston 1974a, Wargo 1983a).

Abiotic Stress Factors

Light

Predisposition to *Armillaria* root disease from inadequate light has been observed in natural forests and plantations, and it has been demonstrated experimentally. *Armillaria* commonly attacks suppressed understory trees, upon which it acts as an ecosystem scavenger (Davidson and Rishbeth 1988, Pearce and others 1986, Rishbeth 1983). While these trees may be more susceptible to *Armillaria* attack because of genetic makeup, they are also affected by the reduced sunlight, which reduces the amount of energy available for defense against pathogens. Susceptibility, therefore, would be influenced by the shade tolerance of the tree species.

Redfern (1978) demonstrated the effects of insufficient light on susceptibility of trees to *Armillaria* in both plantation and greenhouse studies. Dominant and suppressed Scots pine in a 19-year-old plantation were inoculated and examined after 9 months. Similar numbers of dominant (12/15) and suppressed (13/15) trees were infected; however, the severity of infection, as measured by length of root invaded, was greater in the suppressed trees than in the dominant trees. Two suppressed trees were killed.

Inoculation studies with known *Armillaria* species on subdominant trees and suppressed trees growing in reduced light showed that suppressed English oak and Scots pine were infected by *A. mellea*, *A. ostoyae*, and *A. gallica* but not by *A. tabescens* (Davidson and Rishbeth 1988). Only *A. mellea* colonized the healthier subdominant oaks, and only *A. ostoyae* colonized the subdominant pine.

In one greenhouse study, *Armillaria* killed significantly more seedlings of Japanese larch growing under an 8-hr daylength than those growing under a 16-hr daylength for 20 weeks (Redfern 1978). In a second greenhouse study, seedlings of grand fir, western hemlock, and English oak were inoculated and grown under shade (70% light reduction) and compared with seedlings grown in full sunlight (Redfern 1978). Light did not affect susceptibility of western hemlock, which is a shade-tolerant species; 60% of seedlings were killed in each treatment. Shade, however, increased the susceptibility of the less-tolerant species, with 44% and 76% of the fir and 2% and 22% of the oak seedlings killed in full sunlight and shade treatments, respectively. Greenhouse studies with *A. ostoyae* on western

white pine also showed that very young seedlings (3-week-old) were more susceptible to infection if grown under reduced-light conditions (Entry and others 1986).

Temperature

Both high and low temperature extremes can stress trees and render them susceptible to opportunistic organisms. The effects of high temperatures, however, are commonly associated with drought, and distinguishing their individual effects can be difficult. In his report on environment and *Armillaria* root disease, Day (1929) indicated that the fungus attacked trees affected by sun scorch, drought, and defoliation. Sun scorch on leaves is caused by high temperatures associated with dry conditions and can significantly damage trees. Hole (1927a,b) found that drought and sun scorch on the foliage and sunscald on the smooth bark of morinda spruce in India significantly injured the crowns and predisposed the root systems to *Armillaria* colonization. Mortality was greatest on the hot, western and southern slopes and least on the cool, northern sites.

Elevated soil temperature, attributed to a slightly warmer summer climate and opening of the canopy by extensive logging, was proposed as a major factor in birch dieback in eastern Canada and Maine (Redmond 1955). Experimentally elevating the soil temperature by 2°C increased rootlet mortality from 6% to 60%. Trees in stands suffering "birch dieback" were characterized as having progressively greater rootlet mortality as crown vigor decreased. These trees were frequently colonized by *Armillaria*, but the fungus was not considered the primary cause of this decline (Hansbrough and others 1950, Spaulding and MacAloney 1931).

Bliss (1946) found that the greatest resistance to infection and colonization by *Armillaria* occurred at soil temperatures that were most favorable for root growth. Virulence was greatest at lower soil temperatures (10-18°C) on host species with a high soil temperature range for optimum root growth (17-31°C), such as peach, apricot, and geranium. On host species with a low soil temperature range for optimum growth (10-17°C), such as sweet orange, sour orange, orange and rose, virulence was greatest at higher soil temperatures (15-25°C).

Stress from freezing damage and subsequent colonization by *Armillaria* is documented for snowbrush. Severe crown kill of this evergreen shrub occurred in 1963 in Montana during a winter of light snow and after a sudden temperature drop from above freezing to -14°C to -20°C (Stickney 1965). A subsequent survey of snowbrush dieback in the Northwestern United States showed that *Armillaria* was associated with dead and dying clumps of this shrub (Tarry and Shaw 1966). Perhaps the freeze-damage predisposed the shrub to

Armillaria. Subsequent work on this dieback (Tarry 1969) showed that 77% of the declining snowbrush stumps were infected by *Armillaria*. Results of inoculations in healthy plants were poor; less than 5% of 108 inoculation attempts resulted in infections, suggesting that colonization depended primarily on predisposing stress.

Infection and colonization of peach trees by *Armillaria* and other secondary organisms also were attributed (Poole 1933) to sudden exposures to low temperatures (-12°C to -9°C). These were extremes for peach orchards in the Carolinas (United States), and tree mortality ranged from 10% to 100%.

Damage from late spring frosts also predisposes trees to *Armillaria*. In North Carolina, late spring frosts were associated (Beal 1926) with the death of numerous white oaks. Later work indicated that much of this mortality was associated with *Armillaria* and bark insects (Hursh and Haasis 1931). *Armillaria* also infected chestnut trees (probably American chestnut) twice defoliated by late spring frosts (Long 1914).

Trees can also be stressed from events associated with but not directly related to low temperatures. Severe deterioration of an 80-year-old stand of red oak after a severe ice storm was attributed to *Armillaria* which colonized trees weakened by ice damage to their crowns (Dance and Lynn 1963). Hintikka (1974) suggested that Scots pine in plantations were predisposed to *Armillaria* infection by heavy snows that severely bent the saplings. However, *Armillaria* damage was severe in these snow-damaged plantations, perhaps due to increased wounding of the roots that lifted when the trees were bent rather than from direct reduction in tree vigor.

Moisture

Drought is probably the most common stress affecting trees, and at some time during most years trees experience either short- or long-term reductions in soil moisture. In their reviews on the relationship of *Armillaria* with widespread dying-off of forest stands in Europe, Twarowski and Twarowska (1959) and Nechleba (1915) indicate that attack of both conifer and hardwoods by *Armillaria* has been associated with drought since the late 1800's. Parasitism by *Armillaria* on true fir species was reported to increase during dry seasons, while wet seasons favored its saprophytic role (Nechleba 1927). Müller (1921) observed that droughts in the 1890's and early 1900's preceded *Armillaria*-caused deaths of many firs in Germany. Nechleba (1915) suggested that drought was the major factor in predisposing conifers to *Armillaria* and that the fungus "... under normal conditions of moisture and temperature, is a pronounced

and blameless saprophyte.” Falck (1918, 1923) and Hen (1914) observed that drought was also involved in predisposing oaks to *Armillaria*. These early observations of stress-induced susceptibility to *Armillaria* led to the widely held view of the fungus as a secondary pathogen on forest trees.

Later reports also confirm the relationship of drought and *Armillaria*. Biraghi (1949) observed that infection of fir was enhanced during prolonged drought; however, mechanical injury also played a role. In East Africa, radiata pine were killed by *Armillaria* after an extended drought (Anon. 1952). In the United States, drought and subsequent *Armillaria* infection have been reported for western white pine (Ehrlich 1939), eastern hemlock (Secrest and others 1941), and balsam fir (Livingston and others 1982).

Oak decline and mortality in the United States have been frequently associated with drought conditions. Drought, in combination with defoliation from late spring frosts, followed by attack of the stressed trees by *Armillaria*, resulted in large-scale mortality in white, black, red, and scarlet oaks (Hursh and Haasis 1931). Staley (1965) also concluded that drought and defoliation from insects and frost damage predisposed scarlet oak to *Armillaria*. Similar relationships of drought, defoliation, and mortality of oak associated with *Armillaria* root disease were observed in Europe (Falck 1918, Hen 1914, Georgevitch 1926b). The European situation was further complicated by powdery mildew fungi that caused additional defoliation.

Drought also predisposes other hardwoods to *Armillaria*. The severe drought in the late 1950’s through the mid 1960’s in the Eastern United States was considered a predisposing factor in sugar maple decline. *Armillaria* afflicted 46% of symptomatic sugar maple trees in New York State in the early 1960’s (Hibben 1964). Drought is also the most likely initiator of regrowth dieback of eucalypts in Tasmania where *A. hinnulea* and *A. novae-zelandiae* are important secondary pathogens (Kile 1980b, Kile and Watling 1983).

In a review paper on forest declines, Houston (1987) listed seven dieback and decline diseases, their episodic occurrence in North America since the early 1900’s, and their associated stress factors and secondary organisms. Drought was listed as a stress factor in five of the seven diseases discussed; root-rot fungi, predominantly *Armillaria*, were involved in most of the declines. Other associations of drought, forest decline diseases, and *Armillaria* appear in table 8.3.

Root-system development may play some role in the predisposition effects of drought. Observations of *Armillaria* root disease on Scots pine indicated that

root systems of healthy trees were deeper and better developed than those of infected trees. Susceptibility to drought and subsequent infection by *Armillaria* were favored in trees with a shallow, poorly developed root system (Ritter and Pontor 1969). Shallow roots and prolonged drought stress (7 years) were also associated with the decadence of eastern hemlock in Wisconsin (Secrest and others 1941). Declining trees were colonized by *Armillaria*, and root systems of some living trees with “normal” green crowns were also completely colonized by the fungus.

Excess moisture may be as stressful to trees as drought in regards to *Armillaria* root disease. However, the majority of such reports concern hardwood species. Excess soil moisture can cause physiological drought by interfering with water uptake in oxygen-deprived roots. Also, anaerobic conditions in the roots promote the production of ethanol, which can stimulate aggressive *Armillaria* growth (see chapter 3).

An early report on *Armillaria* root disease in the United States (Long 1914) indicated that *Armillaria* attack on various oak species and chestnut was greater and more severe on sites where the soil was wet seasonally. Wet summers also were observed to predispose chestnut species to *Armillaria* infection in Germany and Austria (Bazzigher 1956).

Native oaks in California were apparently infected with but not usually killed by *Armillaria* unless they were irrigated during the summer (Raabe 1966a). Whether irrigation resulted in excess soil moisture that stressed the trees or provided a better environment for more aggressive growth of *Armillaria* was not determined. Dade (1927) observed that high humidity promoted infection in cocoa. High rainfall years and poor soil drainage were also linked to infection of rubber trees in Nigeria (Fox 1964).

Decline of ohia has occurred periodically in Hawaii since 1875 and has been associated with poor soil drainage which, as the trees age, eventually predisposes them to *Armillaria* and other agents (Hodges and others 1986). In Japan, *Armillaria* on larch was related to low host vigor as indicated by annual growth increments, but incidence of infection depended mainly on the amount and duration of excess soil moisture (Kawada and others 1962). Disease was especially severe where larch were growing on soils with a high or perched water table.

Nutrients and Other Soil Factors

Armillaria root disease generally occurs more frequently and severely on nutrient-deficient soils or on

soils with poor physical and chemical characteristics for host growth. *Armillaria*-caused mortality in tea plantations growing in nutrient-deficient soils was considerably greater than in areas where soil fertility was adequate for growth (Butler 1928). In a 32-year-old plantation of eastern white pine in New York, damage by *Armillaria* was associated with low soil nutrients (Silverborg and Gilbertson 1961). Ono (1965, 1970) reported that *Armillaria* caused severe losses in Japanese larch plantations on both upper slopes and lowlands. In both areas, he attributed disease severity to physical and chemical soil characteristics unfavorable for larch.

Some evidence suggests that predisposition by nutrient deficiency depends on which tree species grows where a particular nutrient is low. Reduced nitrogen and phosphorus levels were linked to rapid development of *Armillaria* root disease in conifer plantations in Newfoundland (Singh 1970). Calcium deficiency was related to increased *Armillaria* damage in walnut plantations (Marchal and Foex 1931). Low soil nitrogen and low soil pH were associated with *Armillaria*-caused decay in Douglas-fir, while low soil calcium and phosphorus and high soil potassium were associated with *Armillaria*-caused decay in grand fir (Shields and Hobbs 1979).

Armillaria root disease has been related to extractable aluminum concentrations in soils from sites surveyed for root disease. Browning and Edmunds (1985) found that incidence of *A. ostoyae* on coastal Douglas-fir in the Northwestern United States was generally higher on sites where aluminum levels in the soil were low. Laboratory studies did not conclusively confirm this relationship (Browning 1987). Aluminum inhibited fungus growth but only at high concentrations in buffered media (200 ug/g and above). Fungal growth in coastal soil extracts decreased as extractable aluminum measured in these soils increased, but the correlation was not significant. Inoculated seedlings growing in soils from sites with high and low disease incidence also failed to associate disease incidence with extractable aluminum (Browning 1987).

Relationships between nutrients and susceptibility to *Armillaria* have been demonstrated experimentally. Rate, incidence, and severity of infection of seedlings of Norway spruce, black spruce, Sitka spruce, and Scots pine were greater when they were grown in forest soil with low nutrient levels and low pH (Singh 1983). Three-week-old seedlings of western white pine grown under reduced light and nutrient deficiencies were also infected more frequently and more severely than seedlings grown under adequate light and nutrient supply (Entry and others 1986). With adequate light, more seedlings that received nutrient solutions deficient in

nitrogen or phosphorus were infected than those receiving the complete nutrient solution (Entry and others 1986).

Pollutants

Increased incidence and severity of *Armillaria* root disease associated with SO₂ and other pollutants have been observed (Grzywacz 1973, Jančařík 1961, Kudela and Novakova 1962, Novak and others 1957, Scheffer and Hedgcock 1955). However, reports associating *Armillaria* root disease with pollutants have been inconsistent, and generalizations are difficult. The influence of pollutants is related to the proximity of the forest to the source(s) of pollution. High pollutant levels nearer the source may inhibit the incidence of the disease, but more moderate levels may favor the disease.

In fluoride-damaged conifer stands in Newfoundland (Canada), the pollutant does not favor the disease. Singh and Sidhu (1989) found less *Armillaria* root disease in stands near an emission source than in stands farther away, and mycelial fans and rhizomorphs appeared less vigorous in the more polluted areas.

Grzywacz and Wazny (1973) observed that *Armillaria* root disease in Poland occurred two to three times more frequently in forests situated within or near industrial centers than in remote forests. Over an 8-year period from 1963-1970, area affected by *Armillaria* root disease expanded 3.5 times in forests near industrial centers compared to an overall forest increase of just 1.5 times. However, in young Scots pine plantations the percentage of trees attacked decreased as the proximity to the source and level of SO₂ increased (Grzywacz 1973, Grzywacz and Wazny 1973); incidence also decreased in forests beyond the zone of SO₂ influence. Thus, SO₂ pollution seemingly favors the disease except where the SO₂ levels are very high.

Later studies in Poland failed to support these results (Domanski 1978). He found that *Armillaria* root disease was extremely rare in polluted zones but was quite common in plots uninjured by pollution. Comparing the two studies (Grzywacz and Wazny 1973, Domanski 1978) is difficult because essential details are lacking in both. However, the differences may be related to the species studied, the age of the plantations, and the length of exposure to pollutants. Domanski (1978) suggested that *Armillaria* is suppressed in stands that have been exposed to air pollutants for long periods, but the disease is enhanced in stands that have been recently exposed to and weakened by pollutants.

Recently documented declines in forests of central Europe and eastern North America may or may not be

related to air pollution (Schütt and Cowling 1985, Worrall and Harrington 1988a), but *Armillaria* appears to be associated to some extent. *Armillaria* root disease occurs on some of the declining conifers in German forests (J. Worrall, pers. comm.). In a survey of mortality in spruce-fir forests of Crawford Notch and nearby Bartlett Forest, New Hampshire (United States), mortality attributed to *A. ostoyae* was frequently encountered at low, but not high elevations where pollution levels are higher (Harrington and others 1989, Rizzo and Harrington 1988a, Worrall and Harrington 1988a).

A survey for *Armillaria* root disease throughout the Northeastern United States found that *Armillaria* was associated with decline and mortality of red spruce, but incidence and severity of the disease decreased as severity of the decline and elevation increased (Carey and others 1984). These higher elevation sites are considered to be more polluted because of cloud precipitation (Lovett and others 1982, Scherbatskoy and Bliss 1984). The low incidence and severity of the fungus on declining and dead trees in the upper elevation forests was related to scarcity of rhizomorphs (Wargo and others 1987b). This paucity was correlated with high concentrations of lead (presumably from atmospheric deposition) in these upper elevation sites. Most of the isolates from these sites are *A. ostoyae* (Wargo 1989, and unpubl.).

Laboratory studies on *A. ostoyae* indicate that lead and other heavy metals present in soils of spruce-fir sites at high elevations inhibit both mycelial and rhizomorph growth in culture (Wargo and others 1987a). Rhizomorph production and growth were inhibited by both soluble and insoluble lead at concentrations found in soils at high elevations sites in the Northeastern United States. Inhibition was greater at lower pH levels, suggesting a potential interaction with soil acidification.

Disturbance from Partial Cutting

Partial cutting may intensify *Armillaria* root disease (Edgar and others 1976, Filip 1977, Filip and Goheen 1982, Kile 1981, Koenigs 1969, Redfern 1978). Release from competition should increase the vigor of residual trees, making them less susceptible. However, trees are often stressed upon initial release (so-called "thinning shock") and may succumb to *Armillaria* root disease before the benefits of release are established. Sunscald, winter injuries, wind stress, raised water tables, increased soil temperatures, and other environmental stresses may negatively affect residual trees, at least initially, and predispose them to *Armillaria* root disease. The problem of disturbance from cutting may be compounded because these weakened trees are surrounded by stumps which are food bases for the fungus.

Whether short-term stress from cutting predisposes the trees to existing inoculum or an increased inoculum potential causes increased disease is not clear. For example, western redcedar responded favorably, initially, to a thinning cut; however, 15 years later the residual trees were obviously in poor health (Koenigs 1969). Examination of the root systems of 45 trees indicated that 94% of the trees had rotted roots, and *Armillaria* was the most common fungus observed on or isolated from these diseased root systems. Conversely, residual red spruce in shelterwood cuts were colonized and killed by *Armillaria* within 3 years of cutting (B. Burns, pers. comm.), which would be too soon for appreciable mortality due to an increase in inoculum potential.

Partial cuttings in conjunction with other stresses can kill residual trees. On many sites in south-central Pennsylvania, shelterwood or seed-tree cuts in mixed oak stands followed shortly by gypsy moth defoliation resulted in complete loss of the residual trees (Wargo unpubl., and S. Cook, pers. comm.). These trees were attacked and killed by the two-lined chestnut borer (*Agrilus bilineatus* Weber) and *Armillaria* (Wargo unpubl.). Gottschalk (1989) showed that mortality in managed oak stands was equal to or higher than, but rarely lower than, mortality in unmanaged stands. *Armillaria* root disease and *Agrilus* attack were common on dead trees in these managed stands (Wargo unpubl.).

Partial cutting of red spruce in Northeastern United States also resulted in substantial mortality of the residual trees. These partial cuts were conducted during and shortly after the occurrence of severe droughts (1956-65). Pockets of *Armillaria*-induced mortality began to appear shortly after the cuts, and continued to expand through the early 1970's. These stands were overstocked, slow growing, and had no earlier thinning (W. Kingsley and B. Burns, pers. comm.). Subsequent cutting trials have indicated that where shelterwood cuts or heavy thinnings were conducted in overstocked, stagnated stands, severe mortality from *A. ostoyae* (isolates identified by Wargo unpubl.) struck the residual trees. If early thinnings were conducted, *Armillaria* root disease was not a problem on residual trees, either in subsequent commercial thinnings or in shelterwood cuts. Filip and others (1989) also reported that *Armillaria* root disease was not increased by precommercial thinning in ponderosa pine stands in central Oregon.

How partial cutting affects *Armillaria* root disease will likely depend on the site, the age of the stand when thinned or cut, the pathogenicity of the *Armillaria* species, and the health of the trees when cut.

Biotic Stress Agents

Insect Defoliation

The association of *Armillaria* root disease with defoliation is one of the best documented interactions. This relationship has been consistently observed and reported in forest studies. Also, defoliation has been documented experimentally to predispose trees; the mechanisms by which defoliation predisposes trees to *Armillaria* have been partially characterized.

Colonization of oak species by *Armillaria* after defoliation has occurred worldwide but especially in the United States and Europe. This may be related to both the number of oak defoliators and to several serious exotic insect defoliators that have caused widespread, severe defoliations. In Europe, the roles of *Armillaria*, defoliation, and drought were debated as the cause of widespread oak mortality by several workers (see review by Twarowski and Twarowska 1959). Mortality, primarily of English oak in England, Germany, and Yugoslavia, was related to *Armillaria* root disease and a number of oak defoliators, including insects and powdery mildew (Day 1927a; Falck 1918, 1923; Georgevitch 1926b; Yossifovitch 1926; Osmaston 1927; Robinson 1927). Most authors considered *Armillaria* to be a secondary pathogen.

In the United States, the association of *Armillaria* and defoliated oak has been noted since the early 1900's, and reports have increased in frequency since then. This increase has occurred because the importance of oak in the forest canopy has dramatically increased since chestnut blight, (*Cryphonectria* (*Endothia*) *parasitica* (Murr.) Barr) eliminated the American chestnut. Additionally, gypsy moths (*Lymantria dispar* L.) introduced into the northeastern United States in the late 1800's have caused widespread, severe, and repeated defoliations of oak. Attack of oak trees by *Armillaria* after gypsy moth defoliation was reported in Massachusetts by Baker (1941), but extensive tree losses after defoliation by the gypsy moth had occurred prior to this report (Burgess 1922) and most likely involved *Armillaria* root disease. Defoliation and hence mortality has increased as the gypsy moth infestation has expanded south and westward into areas of greater oak populations. Increased incidence of *Armillaria* root disease after defoliation has been reported in Connecticut (Dunbar and Stevens 1975), New Jersey (Kegg 1971, 1973), and Pennsylvania (Karasevicz and Merrill 1986; Karasevicz and others 1984; Nichols 1961, 1968). This process is occurring presently in Maryland, New York, West Virginia, and Virginia (Twery and others 1990, Wargo unpubl.).

Dunbar and Stephens (1975) suggested, based on presence or absence of the fungus at the root collar, that

Armillaria played only a minor role in oak mortality after gypsy moth defoliation in Connecticut. Wargo (1977), however, showed that presence or absence of mycelial fans at the root collar did not indicate incidence and severity on the whole root system, and that *Armillaria* played a significant role in the mortality of defoliated oaks.

Defoliation by other insects also predisposes oaks to *Armillaria*. In Pennsylvania, *Armillaria* root disease was associated with decline and mortality of red and scarlet oaks defoliated by *Croesia* (*Argyrotoxa*) *semipurpurana* (Kearf.), the oak leaf roller (Staley 1965). In Bulgaria, *Armillaria* attacked oaks defoliated by leaf beetles (Shipchanov and others 1979).

Armillaria also plays a prominent role in the decline of defoliated sugar maples. A series of studies in Wisconsin on "maple blight" showed that defoliation initiated the problem (Giese and others 1964a,b). Ultimate mortality was often attributable to roots and root collars infected by *Armillaria* (Houston and Kuntz 1964). *Armillaria* root disease was also associated with sugar maple mortality in north-central New York after defoliation by the saddled prominent caterpillar, *Heterocampa guttavitta* Weber. (Wargo unpubl. and D. Houston, pers. comm.). Subsequent inoculation trials with an isolate of *A. gallica* on both artificially and naturally defoliated sugar maple showed that successful invasion of the root systems depended on stress from defoliation (Wargo and Houston 1974, Wargo unpubl.).

Armillaria attack after defoliation has also been reported for conifers. In Canada, defoliation by the spruce budworm, *Choristoneura fumiferana* (Clemens), apparently predisposes balsam fir (Sterner 1970, Stillwell and Kelly 1964) and black spruce (Raske and Sutton 1986) to *Armillaria*. Raske and Sutton (1986) found that infection increased from 30% to 85% when defoliation exceeded 80%. Filip (1989b) reported a very low incidence of *Armillaria* root disease in grand fir stands in Oregon that had been defoliated heavily for three years by the western spruce budworm, *Choristoneura occidentalis* Freeman. Based on inoculation studies, he suggested that the involved species of *Armillaria* was not very pathogenic. Increased *Armillaria* root disease also was associated with defoliation of western larch by the larch case bearer (*Coleophora laricella* Hubner) in Idaho (Tunnock and others 1969) and defoliation of Norway spruce by *Epinotia nanaxa* Treitschke in Norway (Austara 1984).

Another form of "defoliation" that occurs periodically is short-rotation, continuous cropping of trees such as that used in aspen management (see chapter 8). Defoliation is sudden and complete, and the tree responds

by producing stump sprouts that perpetuate the root system. The incidence of *Armillaria* increases with the number of successive coppices (Stanosz and Patton 1987a,b; Stiell and Berry 1986).

Other Insects

Increased incidence of *Armillaria* is associated with insects other than defoliators. In Newfoundland (Canada), disease incidence and severity markedly increased in balsam fir stands infested by *Adelges piceae* (Ratz.), the balsam wooly adelgid, a sap-sucking insect (Hudak and Singh 1970, Hudak and Wells 1974). The number of trees infected by *Armillaria* and the severity of infection were directly proportional to the severity of damage by the wooly adelgid.

Beech trees are predisposed to *Armillaria* when they are attacked by *Cryptococcus fagisuga* (Linder.), the beech scale. In this case, the scale predisposes the stem bark to a canker fungus, which then predisposes roots to infection by *Armillaria*.

Hylobius root weevils, *Hylobius warreni* Wood and *H. pinicola* Couper, also have been reported to predispose conifers in Newfoundland to *Armillaria* root disease (Warren and Singh 1970). Incidence of root disease increased in weevil-injured versus uninjured trees for Sitka spruce (15% vs. 4%) and Norway spruce (7% vs. 5%). In red pine, incidence was low and somewhat less (1% vs. 3%) in weevil-injured trees. Because feeding wounds made by these weevils may be important infection courts for *Armillaria* (Warren and Whitney 1951, Whitney 1961), the association with the weevil may not be predisposition in the same sense as with the aforementioned defoliators.

A reverse association of *Armillaria* root disease and bark beetles occurs among the conifers. In these relationships, root diseases, including *Armillaria*, stress the trees and predispose them to attack, colonization, and subsequent killing of the tree by bark beetles (Cobb 1989, Cobb and others 1974, Kisielowski 1978, Maslov and Nizharadze 1973, Secrest and others 1941, Thomas and Wright 1961). Such attacks may be important for maintaining endemic beetle populations (see chapters 8 and 10).

Trees with root disease may not just be more susceptible to successful beetle attack, but also may be more attractive to the insects. Increased production of volatile oils and changes in the chemical makeup of oils in needles of Norway spruce occurred in trees colonized by *Armillaria* and subsequently attacked by *Ips typographus* (L.) (Madziara-Borusiewicz and Strzelecka 1977). At least one volatile oil, myrenetol, is related to attractants and aggregation-pheromone production in bark beetles other than *I. typographus*.

The associations of bark-infesting beetles and *Armillaria* in hardwood trees have not been studied as intensively as in conifers. The two-lined chestnut borer (*A. bilineatus*), which attacks most oaks and various other hosts, commonly attacks trees stressed by drought and defoliation, and is therefore commonly associated with *Armillaria* root disease (Cote and Allen 1980; Dunbar and Stephens 1975, 1976; Kegg 1971, 1973; Nichols 1968; Staley 1965; Wargo 1977). Various roles in tree mortality were assigned to each organism based on its incidence and severity of attack. Both organisms, however, contribute to mortality after stress; and both *Armillaria* and the borer can attack trees independent of each other or in combination (Wargo 1977). Unlike the conifer relationship, *Armillaria* root disease does not commonly predispose oaks to attack by the two-lined borer (Wargo 1977).

Other Diseases

Armillaria occurs commonly with other root pathogens in conifer stands, especially *Phellinus weirii* (Murr.) Gilb., *Heterobasidion annosum* (Fr.) Bref. (*Fomes annosus*) and *Phaeolus schweinitzii* (Fr.) Pat. (Filip 1979, Filip and Goheen 1984, Hansen and Goheen 1989, Hobbs and Partridge 1979, Whitney and Myren 1978; see chapter 8). In many infection centers, *Armillaria* occurred with one or more root pathogens (Goheen and Filip 1980). The pathogens colonized roots of adjacent trees and, in some cases, roots of the same tree. *Armillaria* was commonly associated with *P. weirii*, *H. annosum*, or *Leptographium* (*Ophiostoma*) *wagneri* (Kendr.) Wingf. on grand fir, Douglas-fir, lodgepole pine, and ponderosa pine (Filip and Goheen 1982, Goheen and Filip 1980).

These associations among root pathogens could be coincidental or the consequence of successional relationships. *Armillaria* may colonize Douglas-fir infected with *P. schweinitzii* in the U. S. Pacific Northwest (Hansen and Goheen 1989), but the reverse order of colonization was reported in Britain (Barrett 1970, Barrett and Greig 1985). *Leptographium wagneri*, the causal organism of black stain root disease in conifers in the Western United States, seemed to predispose ponderosa pine, Douglas-fir, and mountain hemlock to *Armillaria* (Goheen and Hansen 1978). *Armillaria* root disease occurred only occasionally at margins of disease centers of black stain root disease, but occurred frequently within the infection centers on trees affected by *L. wagneri*. Similarly, Byler and others (1983) found *Armillaria* on black-stained Douglas-fir within infection centers, but only the black stain fungus on trees at the margins of the centers.

Ceratocystis virescens (Davids.) C. Moreau, the causal organism of sapstreak disease of sugar maple (Hepting 1944, Houston and Schneider 1982, Kessler and Ander-

son 1960), appears to predispose sugar maple to *Armillaria*. Hepting (1944) found *Armillaria* and *Xylaria* root disease fungi commonly on trees with sapstreak disease. The sapstreak pathogen produces abundant volatiles on colonized sugar maple wood; these materials stimulate *Armillaria* growth in vitro (D.R. Houston, pers. comm.).

Foliage diseases can weaken trees by reducing or eliminating leaf surface area available for photosynthesis. Falck (1918, 1923) reported that English oaks in Europe were attacked and sometimes killed by *Armillaria* after they had been defoliated by *Microsphaera quercina* (Schw.) Bunill, the powdery mildew fungus. The trees had been stressed by earlier insect defoliation and drought, and had refoliated; new leaves are susceptible to mildew attack and complete defoliation by the fungus.

In New Zealand, growth loss of radiata pine was related to a combination of needle blight caused by *Dothistroma pini* Hulbary and root disease caused by *A. novae-zelandiae* or *A. limonea* (Shaw and Toes 1977). Sample size and method precluded clarifying the predisposition roles of each organism. However, growth loss of trees attacked by both organisms was greater than the growth losses attributable to each organism alone; only trees infected by *Armillaria* died. This suggests that severity of *Armillaria* attack was enhanced by needle blight.

Beech trees in northeastern North America are, as noted earlier (Ehrlich 1934, Wargo 1983a), predisposed to *Armillaria* attack by beech bark disease (fig. 7.3). Roots associated with stem portions killed by *Nectria coccinea* var. *faginata* are commonly attacked by *Armillaria*. If attack by the scale and canker fungus continues circumferentially, additional roots are attacked by *Armillaria*. This relationship can continue until eventually the tree is killed, girdled above by the canker fungus and below by *Armillaria*. However, progression of the canker disease may cease because of reduced scale populations. In these cases, *Armillaria* becomes established as a decay organism on the initially infected roots but is prevented from colonizing adjacent healthy tissues by vigorous callousing.

Blister rust, caused by *Cronartium ribicola* Fisch., can predispose western white pine to *Armillaria*. Kulhavy and others (1984) found high correlations between percentage of roots infected by *Armillaria* and bark beetle attack, and between percentage of crown killed by *C. ribicola* and bark beetle attack. The authors hypothesized that trees invaded by blister rust were predisposed to *Armillaria*

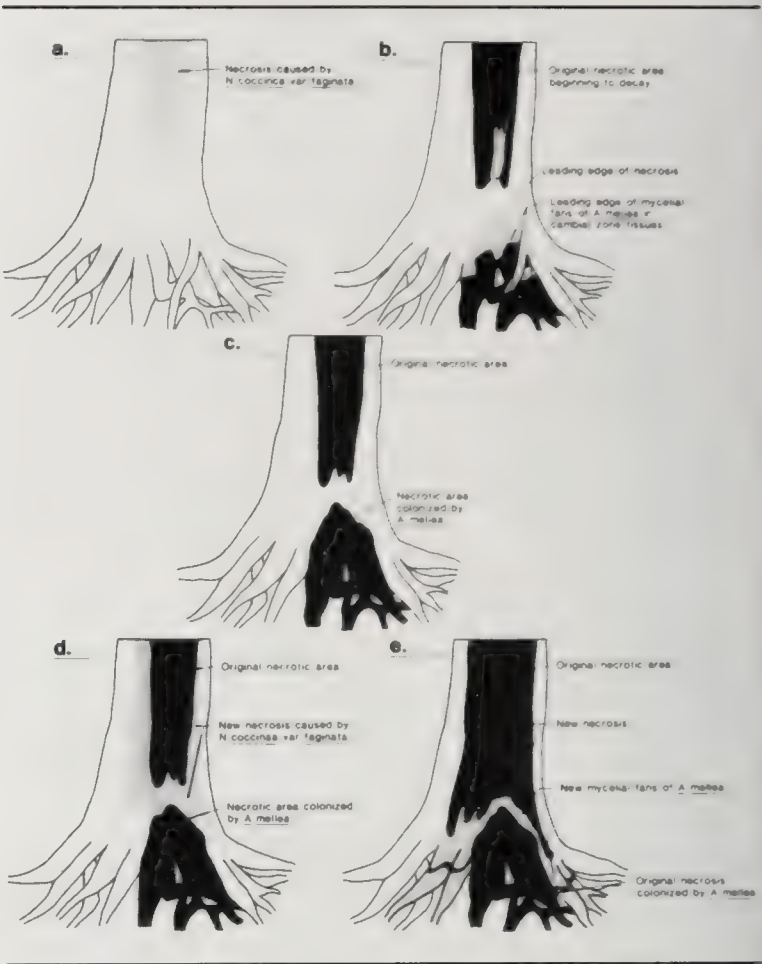


FIGURE 7.3 — Diagram of the lower stem and root-stem base of a beech tree, illustrating the timing and pattern of stem colonization and subsequent necrosis caused by *Nectria coccinea* var. *faginata* and corresponding colonization of the roots by *Armillaria*. a: Initial stem necrosis caused by *Nectria*; b: Necrotic area on roots caused by *Armillaria*; c: Necrotic area on stem in advanced stages of decay; necrotic area in roots completely colonized by *Armillaria* and beginning to decay; d: New stem necrosis caused by *Nectria* adjacent to original necrosis; e: Invasion by *Armillaria* of roots corresponding to area of new stem necrosis (from Wargo 1983a).

root disease, which in turn predisposed trees to attack by bark beetles.

Another major tree disease that predisposes conifers to *Armillaria* is dwarf mistletoe (*Arceuthobium* spp.). *Armillaria* and *H. annosum* were associated with dwarf mistletoes in causing mortality on true firs and pines (Byler 1978). Root pathogens, primarily *Armillaria* and *H. annosum*, in combination with dwarf mistletoe, accounted for 11% to 28% of overall conifer mortality found in surveys in four California national forests (Byler 1978). In Manitoba, Canada, accelerated mortality of jack pine in localized centers in stands affected by dwarf mistletoe is attributed to *Armillaria* root disease (T. Meyer pers. comm.). The problem is concentrated on poor sites with deep sandy soils.

Managing Stress

Controlling dieback and decline diseases that are stress-initiated and involve *Armillaria* focuses on reducing or preventing the effects of the predisposing stress (Houston 1973, 1974b, 1981c). Alleviating or preventing predisposing abiotic stresses such as drought, frost, and waterlogging may be difficult in a forest setting. However, in urban, park, and garden settings, watering (but not overwatering), fertilizing, pruning, mulching, and proper site selection can reduce or eliminate the effects of temperature and moisture extremes. These practices can reduce the chances for infection and colonization by *Armillaria*. For some biotic stress agents, direct control to prevent insect infestations or disease buildup will eliminate the stress and reduce or prevent colonization by *Armillaria*. Direct control of defoliators, such as the spruce budworm or gypsy moth, by spraying insecticides should ultimately reduce mortality caused by *Armillaria*.

Silvicultural practices can be used to regulate species composition, maintain biological diversity, reduce chances for insect pest buildup on selected tree species, and increase host vigor (Houston 1981c). For example, silvicultural techniques could reduce the susceptibility and vulnerability of stands to beech bark disease by reducing the stand's beech component, while at the same time retaining beech trees that are resistant to the beech scale (Houston 1981c). Managing oak forests to control gypsy moths can also lead to reduced *Armillaria* root disease. Forests that are most resistant to defoliation are those with diverse species compositions growing on mesic sites (Houston and Valentine 1977, Valentine and Houston 1979). Maintaining diversity through forest management ensures the perpetuation of forests more resistant to defoliation, and these low-stress forests should be more resistant to *Armillaria* root disease. Partial cutting or thinning may also increase host vigor and resistance to *Armillaria* root disease (see chapter 11). However, as mentioned earlier, partial cutting may stress residual trees and lead to more *Armillaria* root disease in some forest types, so cutting practices may need to be altered.

Conclusions

Predisposing stresses significantly affect the development of *Armillaria* root disease. Even where *Armillaria* functions as a primary pathogen, stress may have some as yet undefined role in disease development. A wide variety of both abiotic and biotic factors may stress a host tree and allow infection and colonization by *Armillaria*. Limited evidence suggests that stress impairs physiological processes critical to resistance and decreases the energy reserves required to sustain the resistance response. At the same time, stress-induced chemical changes provide the fungus with abundant carbohydrate and nitrogen sources, and perhaps other nutrients, that stimulate vigorous growth of *Armillaria*. Alleviating the stress should control *Armillaria* root disease, perhaps by allowing the host to fully express its genetic capabilities to resist infection.

Our understanding of stress-induced susceptibility to *Armillaria* is limited by information regarding distribution of *Armillaria* species, understanding the physiological and pathogenic capabilities of each species, and recognizing the different relationships among various host and *Armillaria* species. We particularly need information about which combinations of pathogen and host have an essential requirement for predisposing stresses, which combinations require no stress to cause disease, and in which combinations disease is merely enhanced by stress. Inoculation studies using several genotypes of each *Armillaria* species and clonal host material, performed in both controlled and natural environments, may provide this information. Species of *Armillaria* must also be identified when disease episodes associated with various stresses are investigated. The concepts presented in this chapter undoubtedly will change as we increase our knowledge and understanding of *Armillaria* species, and of their relationships with host species and climates throughout the world.

Ecology and Disease in Natural Forests

Glen A. Kile, GERAL I. McDONALD, and James W. Byler

A*rmillaria* is unique among the basidiomycete genera that include woody root- and butt-rot parasites. It occurs worldwide in boreal, temperate, and tropical forests, and through diverse parasitic activities it affects a broad variety of host species. Species of the genus are, therefore, a significant consideration in the ecology and management of many natural forests.

Armillaria (as *A. mellea*) was first recognized as a pathogen in plantations and amenity plantings (Hartig 1873b, 1874). Initially, the fungus was often considered to be purely an opportunistic pathogen infecting plants weakened by other biotic or abiotic agents (Day 1929). While Day clearly realized the potential for both secondary and primary pathogenic behavior, he also stated, "It is quite possible that in natural forest the fungus frequently acts in this second (i.e., primary) role, but if that has been observed it does not appear to ever have been recorded." Only in the last 25 years have several *Armillaria* species received wider recognition as important primary pathogens in some natural forests.

Disease in natural forests significantly impacts forest economics, and forest harvesting and management activities may aggravate the endemic disease caused by *Armillaria* species. To minimize disease losses, forest managers must understand the ecology of *Armillaria*. This understanding also improves knowledge of disease development in plantation and amenity plantings on ex-forest sites. The incidence and severity of disease in the former is initially determined by the *Armillaria* species present and its distribution in the primary community. More broadly, the study of *Armillaria* in forests can enhance our general understanding of disease development in wild populations (Burdon 1987).

This chapter examines the ecology and parasitic behavior of *Armillaria* species in natural forests, disease impacts, and the influence of environmental factors and forest management activities on disease expression.

Geographical Distribution of Species

Armillaria is a natural component of the mycoflora of many forests worldwide. The genus has been most intensively studied in temperate regions, and observations and disease records suggest that more species occur and are more abundant in temperate and boreal forests than in tropical forests. Within the latter zone, *Armillaria* appears most abundant and frequent in forests above 500 m although species also occur in the lowlands (Fox 1964). Although the precise altitudinal and latitudinal limits for the genus have not been defined, *Armillaria* is restricted by excessively wet, cold, or dry conditions. These factors also limit host distribution, but not necessarily to the same extent. In western North America, hosts may grow on arid sites where *Armillaria* may be absent (McDonald and others 1987b). This may reflect either the physical environment which prevents infection or survival or, alternatively, that the distance between hosts does not allow spread even if the fungus were to become established.

The best documented geographical distributions are for five *Armillaria* species in Europe (fig. 8.1). For most species, however, distributions are incompletely known. As a consequence of more recent taxonomic studies and better understanding of the ecology of some species, such information can be expected to increase in the future.

Natural distributions are likely to reflect species origins, opportunities or fitness for long-distance dispersal, or adaptation to a particular host or forest type over a long period. Consistent associations are now recognized for a number of species. These include *A. mellea* and *A. ostoyae* present in various hardwood and coniferous forests, respectively, across the northern hemisphere, and *A. borealis* apparently restricted to high-latitude coniferous forests in Europe and Russia (Anderson and others 1980; Guillaumin and others 1985, 1989a; Rishbeth 1982; Terashita and Chuman 1987, 1989). In Australia, Kile and Watling (1983, 1988)



FIGURE 8.1 — Recognized distribution of five *Armillaria* species in Europe (updated from Guillaumin and others 1985).

identified four species associated with different forest types or ecological situations (fig. 8.2). One species, *A. novae-zelandiae*, found in temperate rainforests in eastern Australia, also occurs in New Zealand and possibly South America (Kile and Watling 1983, 1988; Singer 1969). This suggests a long link with southern-beech and other temperate rainforest species.

Within such broad distributions, factors such as altitude may further differentiate species occurrence. In Europe, *A. mellea* and *A. gallica* are regarded as low-elevation species, while *A. cepistipes* occurs at higher elevation (Guillaumin and others 1989a).

In other forested areas, clear patterns of species distribution have not yet emerged and a number of species may coexist. Little data is available for Africa, South America, parts of North America, China, or Siberia.

Although the extension of *Armillaria* species distributions through trade or introductions of infected plant-

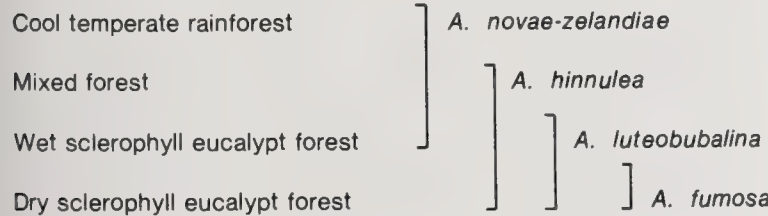


FIGURE 8.2 — Occurrence of *Armillaria* species in major forest types in southeastern Australia, established from basidiome collections during the period 1974-1981. (From Kile and Watling 1983, reproduced courtesy of British Mycological Society).

ing material is possible (Pegler 1986, Piper and Fletcher 1903), no documented example of species naturalization resulting from human activities exists.

Host Range

Collectively, species of *Armillaria* have a very broad host range within the native vegetation where they occur. A large host list has been published for *A. mellea* (Raabe 1962a, 1979a), but attribution of hosts on a worldwide basis to this single species now requires revision. Given our expanding knowledge of *Armillaria* species, we are only beginning to determine the host range of many species in their natural communities, a salutary consideration more than a century after Hartig (1873b) identified *A. mellea* as a parasite.

The nature of the task may be illustrated by *A. luteobubalina*, an Australian species first described in 1978 (Podger and others 1978) and currently one of the few species for which it is possible to prepare a reasonably comprehensive host list. In those forests where it occurs, *A. luteobubalina* infects 81 species in 21 families, including monocots and dicots, and species in each forest strata (table 8.1). The list expands when hosts introduced to Australia are considered (Kile and Watling 1988, Smith and Kile 1981). This emphasizes the continued need for recording hosts so we can fully understand behavior of *Armillaria* species.

Factors determining host preference or specialization in natural forests or whether such phenomena can be clearly defined requires further assessment. Current understanding partly reflects past confusion over species identity, but the issue is undoubtedly complex. Disease caused by the same *Armillaria* species may be expressed differently on various hosts in the same community (e.g., root rot, butt rot, killing). Some species considered pathogenic on hardwood or conifers, respectively, may opportunistically infect both tree types while others can routinely infect plants in both groups. Stress may extend the host range of some species. Details of host specialization/preference are discussed in chapters 4 and 6.

Modes of Behavior in Natural Forests

As facultative necrotrophs, *Armillaria* spp. kill living tissues, then utilize them as a nutrient source. Some species may be obligate saprotrophs, but all species investigated to date appear to have some capacity to infect at least stress-weakened but living host tissue. The generally moist forest environments in which they are active, and defense mechanisms such as pseudo-sclerotial plates and antibiotic production by which species retain control of infected material, may extend

TABLE 8.1 — Hosts of *Armillaria luteobubalina* in various strata of dry sclerophyll eucalypt forest in Australia.

Family	Host Species	Family	Host Species
	Overstory		Groundflora/shrubs
Myrtaceae	<i>Eucalyptus baxteri</i> (Benth.) Maid. & Blakely	Cyperaceae	<i>Gahnia psittacorum</i> Labill.
	<i>E. calophylla</i> Lindley	Dennstaediaceae	<i>Pteridium esculentum</i> (G. Forster) Cockayne
	<i>E. camaldulensis</i> Dehnh.	Dilleniaceae	<i>Hibbertia amplexicaulis</i> Steudel
	<i>E. cypellocarpa</i> L. Johnson		<i>H. hypericoides</i> (DC.) Benth.
	<i>E. diversicolor</i> F. Muell.		<i>H. silvestris</i> Diels.
	<i>E. dives</i> Schau.		<i>H. montana</i> Steudel
	<i>E. globulus</i> (Labill.)spp. bicostata (Maid. et al.) Kirkp.		<i>H. obtusifolia</i> DC.
	<i>E. gomphocephala</i> DC.	Epacridaceae	<i>Leucopogon capitellatus</i> DC.
	<i>E. gummifera</i> (Gaertn.) Hochr.		<i>L. nutens</i> E. Pritzel
	<i>E. macrorrhyncha</i> F. Muell. ex Benth.		<i>L. verticillatus</i> R. Br.
	<i>E. marginata</i> Donn: ex Smith		<i>Styphelia tenuiflora</i> Lindley
	<i>E. melliodora</i> A. Cunn. ex Schau.	Euphorbiaceae	<i>Phyllanthus calycinus</i> Labill.
	<i>E. obliqua</i> L'Herit.	Leguminosae	<i>Bossiaea ornata</i> (Lindley) Benth.
	<i>E. ovata</i> Labill.		<i>Daviesia cordata</i> Smith
	<i>E. patens</i> Benth.		<i>D. decurrens</i> Meissner
	<i>E. radiata</i> Sieb. ex DC.		<i>D. horrida</i> Preiss ex Meissner
	<i>E. rubida</i> Deane & Maid.		<i>D. ulicifolia</i> Andrews
	<i>E. rudis</i> Endl.		<i>Gastrolobium bilobum</i> R. Br.
	<i>E. viminalis</i> Labill.		<i>G. calycinum</i> Benth.
	<i>E. wandoo</i> Blakely		
	Understory	Liliaceae	<i>Dianella</i> sp.
Casuarinaceae	<i>Allocasuarina fraseriana</i> (Miq.) L. Johnson	Myrtaceae	<i>Melaleuca viminea</i> Lindley
	<i>A. huegeliana</i> (Miq.) L. Johnson	Proteaceae	<i>Adenanthos barbigerus</i> Lindley
	<i>A. humilis</i> (Otto & Dietr.) L. Johnson		<i>Dryandra nivea</i> (Labill.) R. Br.
	<i>Casuarina decussata</i> Benth.		<i>D. sessilis</i> (Knight) Domin.
Compositae	<i>Cassinia aculeata</i> (Labill.) R. Br.		<i>Grevillea bipinnatifida</i> R. Br.
	<i>Olearia argophylla</i> (Labill.) Benth.		<i>Hakea lissocarpa</i> R. Br.
Mimosaceae	<i>Acacia dealbata</i> Link.		<i>H. prostrata</i> R. Br.
	<i>A. extensa</i> Lindley		<i>H. ruscifolia</i> Labill.
	<i>A. mearnsii</i> De Wild.		<i>Synnaphea petiolaris</i> R. Br.
	<i>A. melanoxylon</i> R. Br.	Rutaceae	<i>Boronia littoralis</i> R. Br.
	<i>A. pulchella</i> R. Br.		<i>B. spathulata</i> Lindley
	<i>A. saligna</i> (Labill.) H. L. Wendl.	Santalaceae	<i>Leptomeria cunninghamii</i> Miq.
	<i>A. browniana</i> H.L. Wendl.	Sterculiaceae	<i>Lasiopetalum floribundum</i> Benth.
	<i>A. urophylla</i> Benth.	Xanthorrhoeaceae	<i>Xanthorrhoea australis</i> R. Br.
	<i>A. verticillata</i> (L'Hérit.) Willd.		<i>X. gracilis</i> Endl.
Myrtaceae	<i>Agonis flexuosa</i> (Sprengel) Schau.		<i>X. preissii</i> Endl.
	<i>Hypocalymma angustifolium</i> Endl.	Zamiaceae	<i>Macrozamia riedlei</i> (Fischer ex Gaudich.) C. Gardner
Papilionaceae (Fabaceae)	<i>Bossiaea laidlawiana</i> Tovey and Morris		
	<i>B. linophylla</i> R. Br.		
Proteaceae	<i>Banksia grandis</i> Willd.		
	<i>B. seminuda</i> (A.S. George) B. Rye		
	<i>Persoonia longifolia</i> R. Br.		
Rhamnaceae	<i>Trymalium ledifolium</i> Fenzl.		
	<i>T. spathulatum</i> (Labill.) Ostf.		

*Derived from Edgar and others (1976); Kile and Watling (1981, 1988); Kile and others (1983); Pearce and others (1986); Shearer and Tippet (1988).

saprophytic survival. Kile (1980b), Rishbeth (1972b), and Shaw (1975) have isolated *Armillaria* from stumps 40-70 years after cutting (see chapter 4). Some species also act as mycoparasites and mycotrophs, further emphasizing the ecological versatility of members of this genus.

Regarding general life history or ecological strategies (MacArthur and Wilson 1967), *Armillaria* species may be considered as relatively K-selected (the organism has a long individual lifespan and a low reproductive effort) rather than r-selected (the organism uses its energy in a short, fast growth phase accompanied by a high reproductive effort). K strategists tend towards coexistence. The Andrews and Rouse (1982) analysis of plant pathogen life histories in terms of resource allocation and the nature of the parasitic association indicates *Armillaria* species may also exhibit r-selected characteristics particularly relative to the latter. Pathogens which stress plants by reducing photosynthesis were considered relatively K-selected compared with those which induce disturbance by consuming biomass. *Armillaria* species cause host disturbance, but host debilitation is often a prolonged process; in many cases, host and pathogen may coexist for long periods. Individual species may have a broad host range, another feature associated with r-selected organisms.

Within this framework of nutritional and ecological strategies, a number of activities may be recognized for *Armillaria* species in natural forests.

Decomposer

Decomposition in forest ecosystems is effected by the integrated activity of many heterotrophic organisms, both microbial and animal (Swift 1977). The basidiomycetes play a major role in the process by breaking down complex polymeric material such as cellulose and lignin. In many forests, the role of *Armillaria* as a decomposer is its most conspicuous activity.

As a consequence of parasitic activity or disturbance such as logging, windthrow, or fire, *Armillaria* may infect large quantities of roots, stumps, and sometimes logs and other debris on the ground. In many tree species, both sapwood and heartwood may be infected, although in eucalypts infection is restricted to sapwood (Kile 1980b). *Armillaria* causes a typical white rot of infected material (see chapter 5). In the wettest forests, disintegration of the outermost tissues of stumps or logs from protracted decay may leave convoluted shapes preserved within pseudosclerotial tissue. The crunch of collapsing compartments of pseudosclerotial tissue when one walks on logs decayed by the fungus adds an audible dimension to its saprophytic activities.

Frankland (1982) found the basidiomycete biomass in stumps and root material in a temperate woodland represented up to 80% of the total basidiomycete biomass on the site. The contribution of *Armillaria* species to such biomass has never been quantified, but the extensive infection observed in stumps and roots on many forest sites and the often long possession of the substrate suggest that *Armillaria* species contribute significantly to decomposition and mineral cycling within many forests. This decomposer role may also extend to the decay of timber in service, particularly under conditions of high humidity and moderate temperature (Ellis 1929, Erbisch and Harry 1979, Fassatova and others 1974, Findlay 1951).

Mycoparasite

The diversity of resources utilized by *Armillaria* species is illustrated by the parasitism of *A. mellea* on the agaric *Entoloma arbortivum* (Berk. & Curt.) Donk (Watling 1974). Rhizomorphs invade the developing basidiomes of *E. arbortivum*, and the subsequent mycelial development induces aberrant host morphology (carpophoroids). The association appears relatively common in eastern North America. Although Watling (1974) identified the species as *A. mellea*, *A. gallica* may be the most common mycoparasitic species (Watling 1987). This is the only reported example of mycoparasitism involving an *Armillaria* species. The specificity of the relationship is not understood.

Mycotrophic (Mycorrhizal) Associations

Approximately 400 species of achlorophyllous angiosperms have evolved specialized mycotrophic root systems with basidiomycetes (Furman and Trappe 1971). These fungal associations appear necessary for the development and reproduction of the hosts. Species of *Armillaria* have been identified as associates in several achlorophyllous taxa in the Orchidaceae [*Gastrodia elata* Bl. (Kusano 1911); *G. cunninghamii* Hook.f. (Campbell 1962); *Galeola septentrionalis* Reichb.f. (Hamada 1939, 1940; Sagara and Takayama 1978)] and the Pyrolaceae [*Monotropa uniflora* L. (Campbell 1971)]. Most authors have identified the species as *A. mellea*, but recent studies have shown that in Japan *A. mellea*, *A. cepistipes*, *A. gallica*, *A. tabescens*, and possibly *A. borealis* are associated with *G. septentrionalis* (Terashita and Chuman 1987, 1989).

These associations cannot be considered as typical mycorrhizal relationships because the achlorophyllous host plant parasitizes the fungal associate for carbon compounds and nutrients which the fungi obtain from external sources (Björkman 1960, Furman and Trappe 1971, Harley 1969, Kusano 1911, Malins Smith 1952,

Zhuang and others 1983). In some cases, the mycotrophic associate is shared by the roots of the achlorophyllous angiosperm and those of a photosynthesizing plant, allowing the former to indirectly parasitize the latter via a connecting bridge of mycelium or rhizomorphs in the case of *Armillaria* (Campbell 1962, Kusano 1911). Such a tripartite arrangement has been termed epiparasitism (Björkman 1960). While the mycelia involved may not depend on the host for survival, they probably derive some benefits from it. Gogala (1973) found cytokinins from *Monotropa hypopitys* L. stimulated mycelial growth of *A. mellea* and three other macromycetes.

Kusano (1911) demonstrated a well differentiated structural relationship between *Gastrodia elata* and *A. mellea* with both ecto- and endotrophic mycorrhizal features. He observed a balanced antagonism between host and symbiont in the cortical layers of the orchid tuber which involved killing of host cells by infecting hyphae or vice versa, survival of infecting hyphae in living host cells, and histochemical or cytological changes in the cells of host and fungus (see also Liu 1982, Zhang and Dong 1986, Zhang and Li 1980). The mycorrhizal hyphae showed little structural modification compared with rhizomorphic hyphae, and as the fungus could be parasitic on the orchid in some circumstances, Kusano (1911) ranked *A. mellea* as a primitive symbiont. In *G. septentrionalis*, the roots are infected by hyphae and partially differentiated rhizomorphs, and the host obtains nutrients through the digestion of hyphal coils (Hamada 1939). The structural relationship between *Armillaria* and *G. cunninghamii*, on the other hand, parallels that found in both *G. elata* and *G. septentrionalis* (Campbell 1962). The structural and cytological relationships between *M. uniflora* and *A. mellea* (Campbell 1971) have not been investigated.

Armillaria species are not known to form mycorrhizal relationships with photosynthesizing plants. Mejstřík (1969) failed to synthesize mycorrhizae between *A. mellea* and seedlings of Scots pine or Norway spruce in axenic culture.

Necrotrophic Plant Pathogen

The economic significance of *Armillaria* derives from its role as a parasite of woody plants. As a natural component of the mycoflora of native forests, *Armillaria* causes endemic disease, disease which is constantly present to a greater or lesser extent in a particular place, and distinguished from epidemic or sporadic disease (van der Plank 1975). The long coexistence of hosts and pathogens in natural forests favors a state of balance. However, since environmental or biological conditions do not remain constant, fluctuations in disease levels (local epidemics) will occur. Thus, disease caused by

Armillaria species varies considerably in time and space.

Armillaria species may be considered as primary or secondary pathogens (fig. 8.3). As primary pathogens, they cause disease in healthy, vigorous plants which may range from restricted infections of the host tissues (root lesions, stem canker, butt rot) to progressive infections ultimately lethal to the host. As secondary pathogens, *Armillaria* species are opportunists that infect and kill trees which have been weakened by stress factors — the role of *Armillaria* species in dieback and decline diseases in natural forests.

Armillaria Species as Primary Pathogens

The ability of *Armillaria* species to act as primary pathogens in native forest communities has received less attention than their role as pathogens in plantations established on former native forest sites and as secondary pathogens in dieback and decline diseases. Two points may explain this. First, few studies have focused on the ecology of *Armillaria* in natural forests not suffering from lethal *Armillaria* disease. Second, primary disease is not necessarily lethal or to a large degree visible. As fig. 8.3 indicates, primary disease is a continuum from minor root infection to major progressive and often lethal infection; the distinction between various disease categories may at times be somewhat arbitrary.

Non-Lethal Primary Disease: Root Lesions, Cankers, Butt Rot

Armillaria appears to be abundant and widely distributed in many forests and apparently causes little disease (Boyce 1961, Peace 1962). Besides colonizing dead

Primary disease

- (i) Root lesions, or root rot, basal cankers, butt rot.
- (ii) Killing of natural regeneration, mortality decreasing with stand age.
- (iii) Killing of trees of all ages and sizes singly or in patches throughout the life of the stand.

Secondary disease

- (iv) Pre-existing or new infections kill trees weakened by stress either singly or on a stand-wide basis.

FIGURE 8.3 — The nature of disease caused by *Armillaria* species in native forests.

stumps and roots from which they may ramify through the soil, rhizomorphs may also epiphytically associate with living root systems. The fungus can also be a minor but active primary root and butt parasite. A relatively stable balance exists between host resistance and *Armillaria* pathogenicity such that, in the absence of stress, minor infections appear to have little effect on tree or forest health.

Excavation and systematic examination of tree root systems are difficult but instructive. A number of such studies in various places illustrate the common occurrence of *Armillaria* in many forests. Incidence of infected root systems in natural stands of Jack, red, and eastern white pines in the United States varied across sites from 0%-100% depending on species, stand density, and age, and was independent of tree suppression or injury (Christiansen 1938). In the Kenya Highlands, Gibson and Goodchild (1960) showed that 30% of trees surveyed in apparently healthy natural forests had epiphytic rhizomorphs or root infections. Swift (1972) found less infection in Rhodesian woodlands. In Tasmania's wet sclerophyll eucalypt forest, 74% of 300 partially excavated messmate stringybark and mountain ash had epiphytic rhizomorphs or localized root lesions (Kile 1980b). Depending on tree species, 20%-60% of healthy conifers in the northern Rocky Mountains had epiphytic rhizomorphs (McDonald and others 1987b). In Ontario, *Armillaria* root infection of black and white spruce and balsam fir varied from 31%-42%, and was influenced by tree age, soil type, and moisture supply (Whitney 1978b, Whitney and others 1974). The frequent colonization of logging stumps in the forests of southeastern Alaska also indicates a widely dispersed, indigenous *Armillaria* population infecting both stumps and, occasionally, living trees (Shaw 1981b, 1989c).

Armillaria root infection in healthy forests is limited by the hosts. Infections may be localized by resinous lesions and sapwood discoloration in conifers (Buckland 1953; Shaw 1975, 1980; Tippet and Shigo 1981) while in hardwood roots, sapwood discoloration, callus development, or kino formation (eucalypts) may occur (Kile 1980b, 1981; Shearer and Tippet 1988). Successful root infection may result in basal cankers in both hardwoods and conifers (Kile 1981, Koenigs 1969, Pearce and others 1986, Shearer and Tippet 1988) or internal (butt) decay of the stem. These host reactions are described more fully in chapters 5 and 7.

Butt rot caused by *Armillaria* is considered here as primary parasitism because it occurs in living hosts, because although most damage occurs in the heartwood entry may be gained via living root tissue, and because decay within the stem may extend outwards into the inner sapwood. Butt rot reduces wood quality and merchantable volume, and renders trees hazardous through

susceptibility to stem breakage. Both coniferous and hardwood species are affected. Virtually all reports refer to *A. mellea* as the causal agent, but undoubtedly several indigenous species cause butt rot in various forests. These include *A. borealis*, *A. cepistipes*, *A. gallica*, and *A. ostoyae* in the northern hemisphere (Piri and others 1990, Rishbeth 1982) and *A. novae-zelandiae* and *A. hinnulea* in the southern hemisphere (Hood and others 1989, Kile 1980b). Records of *Armillaria* butt rot are summarized in table 8.2.

Stem rots have been most studied in boreal forests, particularly in North America and Scandinavia where they are considered the major cause of disease loss. The incidence of such rot varies within and among host species as determined by tree age, growth rate, stand history, and site factors (Wagener and Davidson 1954, Whitney and others 1983). *Armillaria* has frequently been noted to cause butt rot in these forests, but the subsequent direct economic loss is generally considered minor. This has been attributed to the relatively low incidence of infection and the limited extension of decay above ground level — usually less than 0.50-0.75 m, even after prolonged infection. Mechanical harvesters which shear trees close to ground level may increase the commercial significance of butt rots (Basham 1973). *Armillaria* butt rot has been reported to reduce pulp yields in both conifers and hardwoods (Björkman and others 1964).

Early reports of *Armillaria* causing butt rot of conifers include those of Meinecke (1916) on white fir in Oregon, and Faull (1919) and McCallum (1928) on balsam fir in eastern Canada (table 8.2). Basham and others (1953) found that while *Armillaria* sp. was isolated as frequently from butt rotted balsam fir in Ontario as *Poria subacida* (Peck) Sacc., it was of much less economic importance than the latter as infections seldom extended more than 0.6 m above ground level. In Norway spruce, volume losses to *Armillaria* butt rot were typically less than 10%-15% of total decay volume (table 8.2).

Armillaria butt rot of hardwoods has been recorded for species in 15 genera (table 8.2). While decay may extend further above ground in some species than in conifers (Nordin 1954, Rishbeth 1982), volume losses to butt rot remain minor. Basham (1958) found *Armillaria* butt rot was responsible for 8% of the total merchantable volume loss in quaking aspen in Ontario, while in Alberta it caused less than 2% loss in quaking aspen and balsam poplar (Thomas and others 1960). Greater loss was recorded for sugar maple in Ontario where *Armillaria* butt rot accounted for 24% of total decay volume, and infections extended an average 2 m or more above ground level depending on tree age (Nordin 1954).

TABLE 8.2 — Occurrence of Armillaria butt rot in conifers and hardwoods*.

Host species	Country or region	Importance	Reference
Conifers			
<i>Abies amabilis</i> (Dougl.) Forb.	British Columbia	<0.4% DV	Bier and others (1948)
	British Columbia	4.7% DV	Buckland and others (1949)
	British Columbia	0.1% DV	Foster and others (1958)
<i>A. balsamea</i> (L.) Mill.	Ontario	M	Faull (1919)
	Quebec	M	McCallum (1928)
	North-eastern USA	M	Spaulding & Hansbrough (1944)
	Eastern N.America	7.9% F	Basham and others (1953)
	Quebec	2.3% F	Smerlis (1961)
	Ontario	10.9% F	Basham & Morawski (1964)
	New Hampshire	M	Rizzo & Harrington (1988a)
	Eastern Canada	M	Davidson (1957)
<i>A. concolor</i> (Gard and Glend.) Lindl. ex Hildebr.	Oregon	M	Meinecke (1916)
<i>A. grandis</i> (Dougl.) Lindl.	Idaho	8.3% F	Hudson (1972)
	Idaho	14% F	Maloy & Gross (1963)
<i>A. lasiocarpa</i> Nutt.	British Columbia	<0.4% DV	Bier and others (1948)
	British Columbia	M	Smith & Craig (1970)
<i>A. lasiocarpa</i> var. <i>arizonica</i> (Merr.) Lem.	Arizona and New Mexico	9% F	Hinds and others (1983)
<i>Dacrydium</i> spp.	New Zealand	M	Birch (1937)
			Gilmour (1954, 1966)
			Hood and others (1989)
<i>Larix decidua</i> Mill.	United Kingdom	M	Peace (1938)
	United Kingdom	2.8% F	Greig (1962)
<i>Phyllocladus aspleniifolius</i> (Labill.) Hook.f.	Tasmania	M	Kile (1980b)
<i>P. alpinus</i> Hook f.	New Zealand	M	Gilmour (1966)
<i>Picea abies</i> (L.) Karst.	United Kingdom	M	Peace (1938)
	Sweden	8% DV	Rattsjö & Rennerfelt (1955)
	Sweden	M	Käärik & Rennerfelt (1957)
	Sweden	15% F	Molin & Rennerfelt (1959)
	Denmark	M	Yde-Anderson (1958)
	Denmark	10.3% F	Yde-Anderson (1959)
	United Kingdom	21% F	Greig (1962)
	Sweden	24.3% F (data combined with <i>P.sylvestris</i>)	Björkman and others (1964) [see also references in Hintikka (1974)]
	Fed. Rep. Germany	30% F	Dimitri (1966)
	Fed. Rep. Germany	6% F	Kató (1967a)
	Fed. Rep. Germany	12.7% F	Schönhar (1969)
	Fed. Rep. Germany	11% F	Zycha (1970)
	Finland	5% F	Kallio & Norokorpi (1972)
	Czechoslovakia	10-15% F	Malek (1973)
	Fed. Rep. Germany	M	von Pechmann and others (1973)
	Finland	M	Hintikka (1974)
	Finland	16% F	Kallio & Tamminen (1974)
	Norway	3.5% F	Enerstvedt & Venn (1979)
	Finland	2.4% F	Norokorpi (1979)
	Finland	<8% F	Hallaksela (1984)
	Sweden	<10% F	Stenlid & Wasterlund (1986)
<i>P. glauca</i> (Moench.) Voss	Eastern Canada	M	Davidson & Redmond (1957)
<i>P. mariana</i> (Mill.) BSP	Eastern Canada	M	Faull (1919)
		0.4% F	Basham & Morawski (1964)
<i>P. rubens</i> Sarg.	Eastern Canada	M	Davidson & Redmond (1957)
	New Hampshire	M	Rizzo & Harrington (1988a)
	Ontario	M	Basham (1973)
<i>P. sitchensis</i> (Bong.) Carr.	United Kingdom	M	Peace (1938)
	British Columbia	M	Bier and others (1946)
	United Kingdom	15.8% F	Greig (1962)

TABLE 8.2 — (Continued)

Host species	Country or region	Importance	Reference
<i>Pinus sylvestris</i> L.	United Kingdom	M	Peace (1938)
	Sweden	24.3% F (data combined with <i>P. abies</i>)	Björkman and others (1964)
<i>Podocarpus</i> spp.	New Zealand	M	Gilmour (1954, 1966)
<i>Prumnopitys taxifolia</i> (D. Don) Laubenf.	New Zealand	M	Hood and others (1989)
<i>Thuja occidentalis</i> L.	Ontario	M	Faull (1919)
<i>T. plicata</i> D. Don	United Kingdom	M	Peace (1938)
	British Columbia	M	Buckland (1946)
	United Kingdom	M	Gladman & Low (1963)
<i>Tsuga canadensis</i> (L.) Carr.	Ontario	2.9% F	Basham & Morawski (1964)
<i>T. heterophylla</i> (Raf.) Sarg.	United Kingdom	M	Peace (1938)
	British Columbia	6.4% DV	Buckland and others (1949)
	United Kingdom	M	Gladman & Low (1963)
	Oregon & Washington	7.4% DV	Goheen and others (1980)
	British Columbia	2.6% DV	Foster and others (1958)
Hardwoods			
<i>Acacia dealbata</i> Link.	Tasmania	M	Kile (1980b)
<i>A. melanoxylon</i> R. Br.	Tasmania	M	Kile (1980b)
<i>Acer saccharum</i> Marsh.	Ontario	24.3% DV	Nordin (1954)
	Ontario	20.3% F	Basham & Morawski (1964)
<i>Betula alleghaniensis</i> Britt.	Ontario	10.8% F	Basham & Morawski (1964)
<i>B. pubescens</i> Ehrh.	Sweden	6.0% F	Björkman and others (1964)
<i>Castanopsis</i> sp.	Papua New Guinea	M	Arentz & Simpson (1989)
<i>Fagus grandifolia</i> Ehrh.	Ontario	23.8% F	Basham & Morawski (1964)
<i>Fraxinus nigra</i> Marsh.	Ontario	54.5% F (small sample)	Basham & Morawski (1964)
<i>Leptospermum lanigerum</i> Sm.	Tasmania	M	Kile (1980b)
<i>Liriodendron tulipifera</i> L.	Eastern USA	M	Hepting & Hedgcock (1937)
	West Virginia	10% F	Byler & True (1966)
	West Virginia	9% F	Binns & True (1967)
<i>Lithocarpus</i> spp.	Papua New Guinea	M	Arentz & Simpson (1989)
<i>Nothofagus cunninghamii</i> (Hook.f.) Oerst.	Tasmania	M	Kile (1980b)
<i>Nothofagus</i> spp.	New Zealand	M	Birch (1937)
<i>Nothofagus</i> spp.	Papua New Guinea	M	Arentz & Simpson (1989)
<i>Ostrya virginiana</i> (Mill.) K. Koch	Ontario	9.4% F	Basham & Morawski (1964)
<i>Phebalium squameum</i> (Labill.) Druce	Tasmania	M	Kile (1980b)
<i>Populus balsamifera</i> L.	Alberta	1.6% DV	Thomas and others (1960)
<i>P. tremula</i> L.	Sweden	>10% F	Eklund & Wennmark (1925)
	Sweden	5.5% F	Björkman and others (1964)
<i>P. tremuloides</i> Michx.	Minnesota	M	Schmitz & Jackson (1927)
	Ontario	27% F	Basham (1958) see also Black (1951)
	Alberta	0.9% DV	Thomas and others (1960)
	Ontario	9.2% F	Basham & Morawski (1964)
	Colorado	0.5% DV	Hinds and Wengert (1977)
	Quebec	M	Laflamme & Lortie (1973)
<i>P. trichocarpa</i> Torr. & Gray	British Columbia	3.1% DV	Thomas & Podmore (1953)
<i>Quercus</i> spp.	Eastern USA	M	Hepting & Hedgcock (1937)
	Eastern USA	10% F	Roth & Sleeth (1939)
<i>Tilia americana</i> L.	Ontario	54.5% F (small sample)	Basham & Morawski (1964)

* Covers records from both natural forests and plantations (Chapter 9), although the latter are restricted to European records for *Picea abies*, *P. sitchensis*, *Thuja plicata*, *Tsuga heterophylla*, *Larix decidua*.
M = minor if recorded as such or effects not quantified but appear to be so on the evidence presented and in the sense of causing little loss of merchantable timber volume.
% Frequency = incidence of infection in trees assessed or percentage of identified infections.
% DV = percentage of the total decay volume recorded attributed to *Armillaria* species.

Few observations in natural forests document the specific site and stand factors which might affect the incidence and severity of *Armillaria* butt rot. This reflects the relatively minor contribution of *Armillaria* to butt rot losses, being treated usually as incidental to those of more destructive stem-rot organisms. Birch (1937) considered overstocking may contribute to the high incidence of butt rot in silver beech pole stands in New Zealand. Basham and others (1953) noted that decay caused by *Armillaria* was more frequent in stands on poorly drained sites than in stands on relatively well drained slopes with more hardwoods in the stands.

Most butt rots are believed to develop via root infections. Basham (1958) suggested that in quaking aspen wind stress and frost heave could facilitate the entry of butt rot organisms, with occasional entry through basal wounds. Nordin (1954) found that frost cracks could provide entry points in sugar maple.

Armillaria butt rot may also occur in the same tree with other decay organisms such as *Heterobasidion annosum* (Fr.) Bref. (Kallio and Norokorpi 1972, Molin and Rennerfelt 1959), or *Armillaria* infection may allow host entry for other decay organisms such as *Phaeolus schweinitzii* (Barrett 1970, Barrett and Greig 1984, see chapter 5).

The general effects of butt rot on host growth rates and longevity are poorly understood (Wagener and Davidson 1954) though information on the relative susceptibility of some species to *Armillaria* butt rot has been obtained under plantation conditions (Gladman and Low 1963, Greig 1962). However, these findings may need to be interpreted in relation to the *Armillaria* species involved.

Lethal Primary Disease

Armillaria kills trees in natural coniferous and hardwood forests in different spatial and temporal patterns and with ecological and economic effects of varying significance. As noted earlier, it is part of the continuum of primary disease effects (fig. 8.3). Four such primary disease syndromes may be recognized around the world: (1) *Armillaria* root disease in boreal forests and western North American coastal conifer forests; (2) ring disease of mountain pine in France; (3) root rot of mixed-species conifer forests in western North America; and (4) root rot of dry sclerophyll eucalypt forests in Australia. An additional and historically interesting report of possible primary parasitism, but for which no further information is available, is that of Geschwind (1920), who observed mortality of conifers when common beech was selectively logged from mixed forest in Bosnia and Herzegovina (Yugoslavia).

First three diseases involve mainly coniferous species and a common *Armillaria* species, *A. ostoyae*, al-

though other *Armillaria* species may be pathogenic in boreal and mixed-species coniferous forests. On a qualitative basis the last three appear to be the most significant diseases for their impact on stand structure and progressive disease development. Other common features of these latter three diseases include their occurrence in relatively drier environments, the discontinuous distribution of the pathogens within the affected forests, the apparent greater pathogenicity of the causal *Armillaria* species compared with the same species or different species in wetter forest environments, and the apparent intensification of disease development following harvesting operations.

Root Rot in Boreal Forests and Western North American Coastal Coniferous Forests

Mortality of single or small groups of seedlings or saplings occurs early in stand development of naturally regenerated, moist coniferous forests in North America and northern Europe-Scandinavia (Baranyay and Stevenson 1964; Bouchier 1954; Buckland 1953; Hintikka 1974; Mallet and Hiratsuka 1985; Morrison 1981; Whitney 1978b, 1988a; Whitney and Myren 1978; Whitney and others 1974). Mortality typically commences soon after stand establishment, reaches a maximum at age 10-20 years, and then decreases in frequency, possibly as the food base declines and host tolerance increases. Effects on overall stocking are usually minimal, although the disease pattern may vary in some regions with limited mortality occurring through the rotation. Trees may survive with root and butt infections (Morrison and others 1985a, Whitney 1988a, Whitney and Myren 1978, Whitney and others 1974). Disease expression may sometimes be associated with stress (Buckland 1953, Baranyay and Stevenson 1964).

A number of *Armillaria* species occur in affected forests, although most disease appears coincident with the presence of *A. ostoyae* (Dumas 1988, Mallet 1989, Morrison and others 1985a, Whitney 1988a). Beyond the natural range of this species or where its distribution is limited, disease is less prominent. Thus in southeastern Alaska forests, where less pathogenic species such as *A. sinapina* may be widely distributed, little killing is evident in regeneration stands (Shaw 1981b, Shaw and Loopstra 1988). *Armillaria borealis* and *A. cepistipes* cause minor mortality and butt rot in Finnish forests (Korhonen 1978, Piri and others 1990).

Ring Disease of Mountain Pine

In relatively undisturbed 120- to 150-year-old mountain pine forests at 1,600-2,200 m in the eastern Pyrénées, mortality from *A. ostoyae* is extensive and chronic (Durrieu and others 1981, 1985; Durrieu and Chaumeton 1988). Killing may be diffuse but most

characteristically occurs in scattered but clearly delimited rings with a marginal zone of dying and dead trees (fig. 8.4). Ring diameter may reach more than 120 m and may expand 1 m per year. Historical ring development, followed on aerial photographs taken over a 36-year period (Durrieu and others 1981), indicates some rings show intermittent development while others cease expanding and gradually disappear. Following stand opening, mountain pine begins regenerating and is only moderately susceptible to *A. ostoyae*. A successional sequence occurs in the understory/ground flora until the forest returns to a pre-disease form.

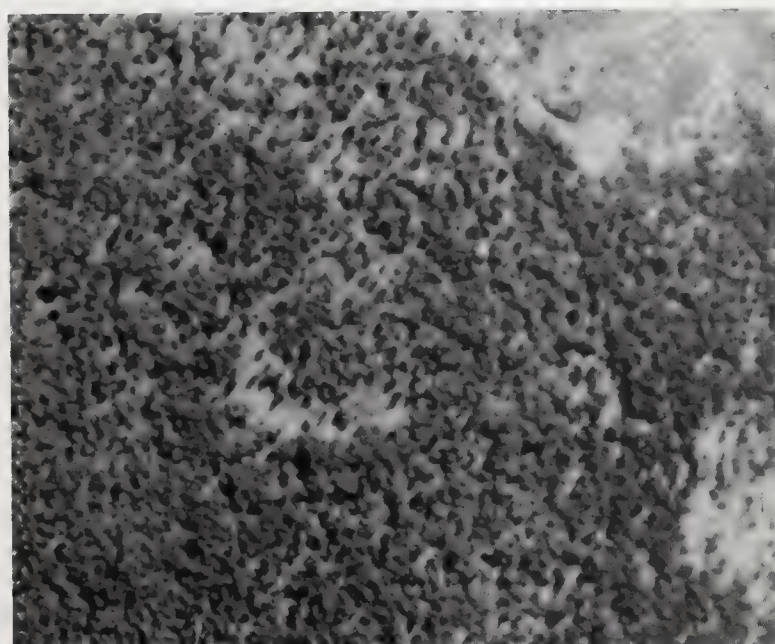
The origin of the rings, the means of pathogen spread within them, and the factors controlling their initiation are poorly understood. The affected forests occur on light-textured, shallow soils, often on steep slopes; rainfall is relatively low (600-750 mm per annum), and bark beetles may act as a stress agent (Torossian 1984). However, the long-standing and strongly patterned nature of the disease and the infection and killing of provenance broom, an understory species, supports *A. ostoyae* as the primary disease cause. Durrieu and others (1985) suggested the fungus is part of the forest's natural ecology, leading to the regeneration of the dominant tree species. While the disease is most severe in the Cerdagne region of France, it also extends westwards into drier transitional forests and may also occur in other parts of the range of mountain pine (Brang 1988).

Armillaria Root Disease in Mixed Coniferous Forests of Western North America

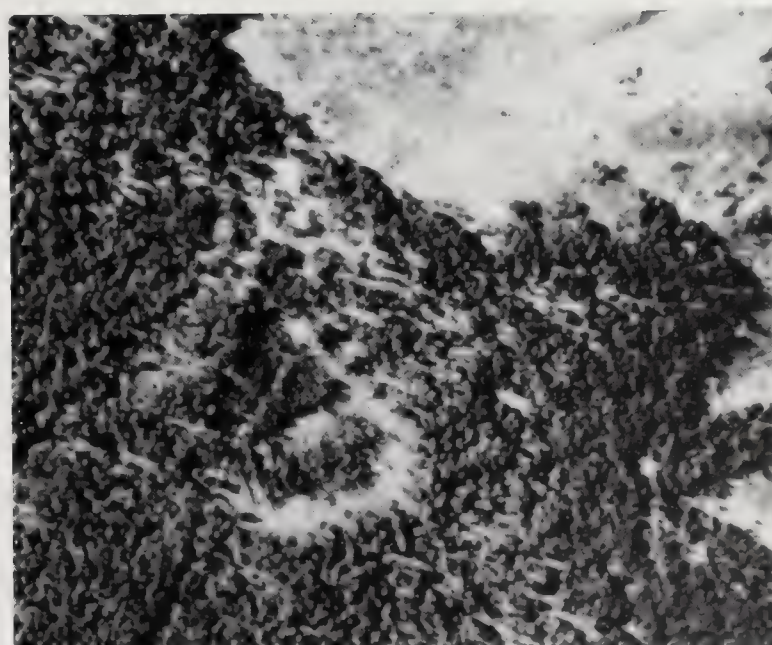
Lethal primary disease affects hundreds of thousands of hectares of natural coniferous forests in western North America. The primary documented areas of forest management concern, where *Armillaria* root disease occurs most extensively and severely, are eastern Oregon and Washington, northern Idaho, western Montana, and the southern interior of British Columbia. The disease is also recognized in the central and southern Rocky Mountains (Wood 1983). In these drier, interior forests, continuing mortality in all age classes is common in many stands; understocked stands may result from multiple disease centers. *Armillaria* root disease has been known for many decades in these forests (Ehrlich 1939; Hubert 1918, 1931, 1950, 1953) but has received minimal attention until the mid 1970's largely because the overall impact was not appreciated.

Smith (1984) estimated the average annual volume losses to five major root diseases [*Phellinus weirii* (Murr.) Gilb., *H. annosum*, *Armillaria* spp., *Phaeolus schweinitzii*, and *Ophiostoma wageneri* (Goheen: Cobb) Harrington] throughout the western United States to be 6.7 million m³, or 18% of the total annual mortality.

While the proportion of this loss due to *Armillaria* root disease cannot be determined, local severity has been evaluated. Shaw and others (1976a) found volume loss to *Armillaria* in a ponderosa pine stand in south-central Washington to have increased from 9 m³ per ha in 1957 to 24 m³ per ha in 1971. In a mixed-conifer stand in southern Oregon, Filip (1977) found 7% of trees comprising 32% of the standing volume were infected with or killed by *Armillaria*. Filip and Goheen (1982, 1984) found annual mortality of more than 3 m³ per ha in other situations. In Montana, a root disease patch in a Douglas-fir stand contained 82% less timber volume per 0.4 ha than the adjacent healthy stand (Byler unpubl.). In British Columbia's interior cedar-hemlock zone, annual timber losses caused by *Armillaria* root



A



B

FIGURE 8.4—Development of ring disease in mountain pine forest, Pyrénées, France. A. Photographed in 1942. B. Same area photographed in 1962. (G. Durrieu)

disease were estimated to be 105,000 m³ (Taylor 1986). Volume growth of Douglas-fir infected by *A. ostoyae* in four stands in southeastern British Columbia decreased significantly as disease severity, measured by basal resinosis, increased from infected stem bases (Bloomberg and Morrison 1989).

Armillaria was also recognized as a major cause of stand damage in other ground and aerial surveys which have recorded incidence and area of root disease centers (Williams and Leaphart 1978). James and others (1984) estimated active root disease centers, mainly attributed to *Armillaria* and *Phellinus weirii*, occupied almost 32,000 ha (about 1% of the total commercial forest land) of seven national forests in the northern Rocky Mountains. A detailed study of one of those forests, the Lolo, found 123,255 ha (18.8% of the total forest) were diseased, of which 8,011 ha (1.2%) were unstocked patches (Byler and others 1990).

Besides timber loss and the creation of unproductive areas through chronic infection, particularly where susceptible hosts are climax (McDonald and others 1987a), *Armillaria* root disease may change species composition, create hazardous trees in recreation forests, and affect the choice of silvicultural system.

Armillaria ostoyae (NABS I¹) (Morrison and others 1985a, Wargo and Shaw 1985) and possibly NABS X (McDonald unpubl.) are pathogenic on conifers in these interior western forests, although *A. ostoyae* is considered the most widespread and aggressive. Additional taxonomic or biological species known to be present in western North America are *A. sinapina* (NABS V), *A. gallica* (NABS VII), NABS XI (*A. cepistipes?*), and NABS IX (Anderson and Ullrich 1979, Morrison and others 1985a, Shaw and Loopstra 1988, Wargo and Shaw 1985). The latter two species have been collected infrequently. Some of these species may act as secondary pathogens.

Where they occur, *Armillaria* species have a complex interaction with about two dozen conifer species. Data on mortality rates resulting from root disease caused by *Armillaria* in different community types and geographic areas are lacking, although observations indicate Douglas-fir and true fir are the most susceptible (Hagle and Goheen 1988, Morrison 1981). Exceptions to this occur in south-central Washington where ponderosa pine is most susceptible and Douglas-fir appears tolerant, and possibly in some other areas where Engelmann spruce (McDonald and others 1987b) and western hemlock appear very susceptible (Morrison 1981). Root disease may also afflict hardwood shrubs (Adams 1974; McDonald and others 1987a,b; Morrison

1981; Shaw 1975; Tarry and Shaw 1966; Williams and Marsden 1982).

In individual stands, mortality often begins within a few years of regeneration and may continue throughout the rotation, particularly in Douglas-fir/true fir forests. For other species, such as western redcedar, mountain hemlock, western larch, western white pine, ponderosa pine, and lodgepole pine, damage tends to diminish with stand age beyond 20-30 years. Disease occurrence varies from individual infected trees (fig. 8.5) to patches (fig. 8.6) of tens of hectares (Byler unpubl., Filip 1977, James and others 1984, Smith 1984, Wargo and Shaw 1985). Patches typically contain conifer regeneration, brush, or grass and have a perimeter of dead and dying trees. Rate of disease spread in a ponderosa pine stand was 1-2 m per annum (Shaw and Roth 1976), but in a Douglas-fir stand less than 0.25 m per annum (Byler unpubl.). Typical infection foci are usually occupied by 1-3 *Armillaria* genotypes (Adams 1974, McDonald and Martin 1988, Shaw and Roth 1976). The dynamics of disease within infection centers and across rotations in these mixed-conifer forests is discussed further in chapter 10.

Armillaria frequently causes damage concomitant with other root-rot pathogens of mixed-conifer forests, particularly with *Phellinus weirii* (Filip and Goheen 1984, Goheen and Filip 1980, James and others 1984, Miller and Partridge 1973, Williams and Leaphart 1978), but also with *O. wagneri* (Cobb and others 1974) and *H. annosum* (F. Cobb pers. comm.). *Armillaria* may be active on the same site or in the same root system as other pathogens. Hansen and Goheen (1989) attributed these associations to chance and to primary-secondary relationships, but the roles have not been adequately defined.

Armillaria infection and other root diseases predispose some conifers to bark beetle infestation (Hertert and others 1975, Hinds and others 1984, James and Goheen 1981, Kulhavy and others 1984, Lane and Goheen 1979, Lessard and others 1985, Partridge and Miller 1972, Tkacz and Schmitz 1986). *Armillaria* root disease may be an important factor in the survival of endemic populations of some bark beetle species. Hinds and others (1984), Lessard and others (1985), and Tkacz and Schmitz (1986) associated such populations of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) with *Armillaria* infection in ponderosa and lodgepole pine stands in South Dakota and Utah, respectively. Interaction between bark beetles and *Armillaria* root disease is considered further in chapter 10.

Western North America is marked by complex landforms and specific associations of plant communities. Large variation in elevation, aspect, slope, altitude, and

NABS (North American Biological Species) as described fully in chapters 1 and 2.



A



B

FIGURE 8. 5— Armillaria root disease killing individual trees near infected stumps in a mixed-species conifer forest in western North American. A: Ponderosa pines; B. Grand fir.



FIGURE 8.6—Armillaria root disease center in virgin coniferous forest in western North America. The lowermost center covers nearly 8 ha (20 acres).

soil type has produced an elaborate mixture of forest ecosystems with widely differing levels of vulnerability to Armillaria root disease. Root disease centers have been associated with particular forest habitat types (Byler and others 1986, 1990; McDonald 1990;

McDonald and others 1987a,b; Williams and Marsden 1982).

Armillaria root disease probably played an important role in forest succession and the determination of stand composition and structure on many mixed-conifer forest sites prior to European settlement (Byler 1984, Byler and others 1990, Hagle and Goheen 1988, Haig and others 1941, Shaw and Roth 1976, Wargo and Shaw 1985). *Armillaria ostoyae*, for example, accelerates succession in interior British Columbian forests especially on wetter sites. There, the pioneer species (usually Douglas-fir or lodgepole pine) is killed and the openings fill with shade-tolerant western hemlock or western redcedar after Douglas-fir, or subalpine fir after lodgepole pine. These species are not markedly less susceptible to *A. ostoyae* but appear to be more tolerant, more frequently restricting infection to root lesions and butt rot (Morrison 1981). Williams and Marsden (1982) suggested a similar role for *Armillaria* and *Phellinus weirii* in the succession on northern Idaho sites where western hemlock was climax. Disease is also evident in other forests undisturbed by human activity (Haig and others 1941, Wargo and Shaw 1985).

Armillaria Root Disease in Dry Sclerophyll Eucalypt Forests

As a primary pathogen, *A. luteobubalina* affects many eucalypt and understory species in dry sclerophyll mixed-species eucalypt forests in central Victoria, and in karri and jarrah forests in southwestern Western Australia (Kile 1981, Kile and others 1983, Pearce and others 1986, Shearer and Tippet 1988). The affected forests occur between 300 m and 1,200 m altitude on soils of variable fertility, and receive annual rainfall of 700-1,200 mm. Most have a long history of logging. Hosts in these forests include at least 81 eucalypt, understory, and ground species (table 8.1).

The evidence for the primary pathogenicity of *A. luteobubalina* includes the constant association of the fungus with disease, a pattern of contagion consistent with that for an organism dependent on a woody food base, a correlation between infection and symptom development in large trees, and pathogenicity of the fungus in pot and field inoculations of some host tree species (Kile 1981, Pearce and others 1986, Shearer and Tippet 1988).

In Victorian forests, diseased trees tend to occur in roughly circular foci although the pattern of disease development is often obscured by multiple infection, cutting, and burning (fig. 8.7). Within patches, which may range from a few trees to 1 ha or more, the disease usually shows progressive outward expansion, with more recently dead and dying trees towards the margin and older dead and often wind-thrown trees towards the center. The chronic nature of infection is apparent by the death of eucalypt or understory regeneration that was established following death or removal of the previous strata. Typically, *A. luteobubalina* or other *Armillaria* species are not found in healthy forest surrounding diseased areas. Similar disease development occurs in jarrah forest. In karri forest, the disease is most active in young stands; with increasing stand age, mortality is restricted to suppressed or subdominant trees although larger trees may be infected (Pearce and others 1986).

Young infected trees often die suddenly with a major proportion of their foliage intact. In contrast, large, mature trees generally show progressive crown die-back before eventual death. Some trees develop basal cankers from infection, which limit fungal spread and promote host survival (Kile 1981). The fungus forms few rhizomorphs in forest soils, and underground spread between hosts occurs via root contacts at an average rate of 1-1.5 m per annum (Kile 1983b).

Several thousand hectares of Australian eucalypt forest are seriously affected by the disease (Edgar and others



FIGURE 8.7 — Aerial view of *Armillaria luteobubalina* root disease center in dry sclerophyll eucalypt forest, Victoria, Australia.

1976, Shearer and Tippet 1988). Edgar and others (1976) estimated mature stands with moderate to severe disease had respective sawlog increments of about one-half and two-thirds that of an average healthy stand, with growth losses of 0.3-2.0 m³ per ha per year depending on site and disease severity. Besides these losses, scattered and small patch mortality is evident in regrowth stands. In 30-year-old regrowth messmate stringybark, with 51-75% of ground-level stem circumference infected by *A. luteobubalina*, average monthly girth increment was only 41% of that of healthy trees (Kile and others 1982).

The wide distribution of *A. luteobubalina* in southern Australia and its intimate association with eucalypt forest communities indicate that it is indigenous. While Kile (1983a) reported evidence of its pathogenic activity in unlogged eucalypt forest, the greatest incidence and severity of disease has been observed in selectively logged forests (Edgar and others 1976). Strong relationships exist between infected stumps and disease incidence (Edgar and others 1976, Kellas and others 1987, Kile 1981, Pearce and others 1986). Though disease is endemic, logging apparently alters the balance between host and pathogen toward more severe local epidemics.

Armillaria Species as Secondary Pathogens

Biotic or abiotic stress of natural forests or individual trees (see chapter 7) within them may transform indigenous *Armillaria* species into vigorous secondary pathogens. This phenomenon is most notable in forests where, prior to stress onset, disease is restricted to epi-

phytic associations, root lesions, and butt rot. This secondary role has been recognized since early this century (Nechleba 1915; see also reviews by Day 1929 and Twarowski and Twarowska 1959) and has often dominated views of the pathogenic behavior of *Armillaria* species (Day 1929, Gremmen 1976).

Virtually all historical reports of secondary pathogenesis refer to *A. mellea*, but many other species also act in this manner. The identity and relative importance of species of different pathogenicity in broadscale secondary diseases such as those shown in table 8.3 therefore require reappraisal.

Although forest diebacks and declines are episodic diseases of varying etiology, all share a causal complex that begins when tissues of healthy trees are altered or predisposed by stress and culminates when those tissues are invaded and killed by facultative parasites (Houston 1973, 1982, 1984, 1987). Because infections by weakly pathogenic organisms are unsuccessful or restricted in the absence of stress, and because in the absence of these organisms trees usually recover with the abatement of stress, organisms of secondary action such as *Armillaria* species are an integral component of the disease syndromes. This does not imply, however, that stress alone cannot kill trees (Houston 1987).

Stress factors include insect damage, primary pathogens, drought, waterlogging, fire, temperature extremes, air pollution, or silvicultural treatments. These stresses may be either protracted or relatively ephemeral, and they may occur months or even years prior to eventual tree mortality. Not all stresses enhance pathogenic activity, however, and some air pollutants probably have an adverse effect on the fungus itself, restricting its ability to take advantage of weakened hosts (Singh and Sidhu 1989).

The prominent role of *Armillaria* species in diseases such as those shown in table 8.3 results from their extensive natural distribution in the stress-affected forests and their primary infection of or epiphytic presence on many root systems prior to the advent of stress. The fungus is thereby able to take advantage of changed circumstances to spread quickly from existing infections or establish new ones. For example, regarding dieback of regrowth messmate stringybark and mountain ash in Tasmania, *A. hinnulea* and/or *A. novae-zelandiae* usually infected a large proportion of each tree's root system at the time of death. Excavations, however, indicated that in healthy forest at least 70% of trees had minor root infections or epiphytic rhizomorphs (Kile 1980b, Kile and Watling 1983). In this and many other diebacks and declines, *Armillaria* is probably responsible for the ultimate death of many trees.

Unlike lethal primary disease caused by *Armillaria* species, where dead and dying trees are usually clustered in expanding foci, the pattern of mortality in dieback and decline diseases is typically more variable, ranging from essentially random to more site or topographically related patterns. *Armillaria* infection is less readily associated with identifiable food bases. The distribution of different *Armillaria* species may explain variations in infection and subsequent patterns of mortality, because species of different pathogenicity may invade root systems at different stages of host debilitation (Guillaumin and others 1989a). The susceptibility of individual trees or stands to infection will be mitigated by site and soil factors and tree vigor.

Experimental studies have demonstrated the increased susceptibility of various tree species to infection when stressed by defoliation, suppression, reduced light intensity, adverse soil moisture conditions, or nutrient supply (Davidson and Rishbeth 1988, Entry and others 1986, Ono 1970, Redfern 1978, Wahlstrom and Unestam 1989, Wargo 1972, Wargo and Houston 1974). Increased susceptibility is related to biochemical changes in the host induced by stress, which lowers host resistance and stimulates development of the fungus. Individual stress factors and their effects on pathogenesis by *Armillaria* are fully discussed in chapter 7.

Dispersal and Distribution

The spatial development of *Armillaria* populations in natural forests ranges from the discontinuous distribution of discrete genotypes of one species, to a mosaic of genotypes to which one or more species may contribute. Through the infection of living hosts, stumps, and roots and the proliferation of rhizomorphs, the latter situation can be equated to a continuous distribution, although even in multi-species populations individual species may have restricted occurrences. Discontinuous distributions appear more typical of temperate, Mediterranean, and tropical forests while continuous distributions are more evident, although not omni-present, in boreal and cool temperate forests. However, better quantification of spatial distributions are required in relation to both *Armillaria* species and forest type.

In boreal and temperate forests, genotypes of different *Armillaria* species have been identified and mapped using alleles of the incompatibility (mating) genes as genetic markers or by intraspecific pairings of diploid forest isolates (see chapter 2).

Dispersal and distribution occur via basidiospore infections that create new infection foci and vegetative growth that expands the local distributions of particular genotypes. Local expansion may proceed by

TABLE 8.3 — Examples of diebacks and declines in natural forests in which *Armillaria* species were recognized as important secondary pathogens.*

Disease and primary host	Major initiating stress	Location	Time frame	Reference
Alaska yellow-cedar dieback(<i>Chaemaecyparis nootkatensis</i>)	Unknown	Southeast Alaska	early 1900s to present	Frear (1982) Shaw and others (1985) Hennon and others (1990)
Dieback and mortality of coniferous species	a,c	Eastern Canada	late 1960s-early 1980s	Hudak and Singh (1970) Hudak and Wells (1974) Raske and Sutton (1986)
Birch dieback (<i>Betula alleghanensis</i>)	a,c,f,g	Northeastern North America	mid 1930s-late 1950s	Spaulding and MacAloney (1931)
Oak declines (<i>Quercus</i> species)	a,c,d	1) Europe	regional occurrences during this century	Baumgarten (1912) Hen (1914) Falck (1918) Georgevitch (1926b) Day (1927a) Stolina (1954) Petrescu (1974) Guillaumin and others (1983)
	a,c,d,g	2) Midwest and eastern USA		Macaire (1984) see reviews by Staley (1965) and Houston (1987) Wargo (1977)
Ohia decline (<i>Meterosideros polymorpha</i>)	b,e	Hawaii	mid 1950s-early 1970s	Laemmlen and Bega (1974) Hodges and others (1986)
Pole blight (<i>Pinus monticola</i>)	a	Western USA British Columbia	1930s-1950s	Hubert (1950, 1953) Leaphart and others (1957)
Regrowth dieback (<i>Eucalyptus regnans</i> , <i>E. obliqua</i>)	a,c	Tasmania	regional occurrences early 1960s-present	Kile (1980b)
Sugar maple declines (<i>Acer saccharum</i>)	a,c,f	Eastern North America	regional occurrences 1950s-present	Houston and Kuntz (1964) Wargo and Houston (1974)
* The derivation of the table arrangement and some data from Houston (1987) is acknowledged.		Stress factors a water deficit/high temperature b poor drainage/water excess c defoliation by insects		d defoliation or damage by fungi e nutrient imbalance f logging disturbance g low temperature damage

rhizomorphs or mycelial growth through and between contacting root systems. The role of basidiospores as inoculum and the involvement of rhizomorphs in spread and infection are considered fully in chapter 4, and comment here is restricted to points particularly relevant to these processes in natural forests.

Basidiospores

Although the potential epidemiological importance of basidiospore infection has long been recognized (Boyce 1919, Rishbeth 1964), the evidence for its importance in natural forests remains circumstantial

based on the detection of multiple genotypes and unique combinations of mating alleles (Kile 1983b, Korhonen 1978).

As with many other macromycetes, spore production by *Armillaria* basidiomes may be prolific and the period for potential basidiospore infection relatively long. Rishbeth (1970) recorded deposition rates of up to 1,000 viable basidiospores per dm² per min. close to basidiomes. Basidiospores have also been trapped from the air on screens and on freshly cut wood (Hood and Sandberg 1987, Molin and Rennerfelt 1959, Rishbeth 1970, Swift 1972). Basidiome production of some

Armillaria species may extend over several months (Fedorov and Bobko 1989, Kile and Watling 1981, Pearce and others 1986, Rishbeth 1970, Shubin 1976). Shaw (1981a) found basidiospores could remain viable on the outer bark of conifers over an Alaskan winter.

Environmental factors, particularly moisture, host, and *Armillaria* species, may influence spread and infection by basidiospores (Rishbeth 1970). In the relatively dry interior forests of western North America, few genotypes of *A. ostoyae*, and the large areas occupied by some of them, suggest limited opportunities for basidiospore infection (Shaw and Roth 1976). Similarly, in dry sclerophyll eucalypt forest in Victoria, where 36 genotypes were found in 24 ha, Kile (1983b) estimated the rate of basidiospore infection for *A. luteobubalina* could average less than one per year. In wet sclerophyll eucalypt forest in Tasmania, 46 genotypes of *A. hinnulea* were isolated in 1.1 ha, suggesting relatively frequent basidiospore infection in this forest type (Kile 1986). A situation comparable to the latter probably exists in deciduous forests in the Northeastern United States, Finnish coniferous forests, and New Zealand hardwood-podocarp forests where moisture conditions are favorable for frequent and abundant basidiome production (Anderson and Ullrich 1979, Hood and Sandberg 1987, Korhonen 1978).

Because of our poor knowledge of basidiospore infection courts and the potentially large number of factors which may influence the incidence of basidiospore infection, further experimental studies of the process are needed.

Rhizomorphs and Root Contacts

Both rhizomorphs and root contacts are important for spread and infection in natural forests. The actual contribution of rhizomorphs to these two processes probably depends on the forest environment and the characteristics of the rhizomorphs of the particular *Armillaria* species (see chapters 4 and 6), but they are not obligatory for either spread or infection.

Infection via root contact has received little attention in the past, but its efficiency in some forests suggests it could contribute to spread even in situations where rhizomorphs are present. *Armillaria luteobubalina* spreads almost exclusively by this means in Australian eucalypt forests even though it produces rhizomorphs on agar and in pot culture (Kile 1981, Morrison 1989, Pearce and others 1986, Podger and others 1978, Shearer and Tippet 1988). Rhizomorphs also are formed rarely in many tropical forests (Butler 1928; Dade 1927; Swift 1968, 1972).

The lack of rhizomorphs in native forest soils has been attributed to unfavorable physical environments for their initiation and growth (Pearce and Malajczuk 1990a,

Rishbeth 1968) or to inhibitory compounds in the soil (Olembo 1972, Swift 1968). Pearce and Malajczuk (1990a) showed limited rhizomorph development of *A. luteobubalina* in karri forest soils in Western Australia related to unsuitable combinations of soil temperature and soil moisture levels for rhizomorph growth during much of the year. Whether this explanation is adequate in other forests where rhizomorphs are absent remains to be determined.

Spatial Distributions

Over time, dispersal processes contribute to varied patterns of genotype and species distribution. These patterns appear to form a continuum from the simple to the complex depending on the frequency of new infections and the number of *Armillaria* species. In coniferous forests in western North America and dry sclerophyll eucalypt forests in Victoria, relatively few genotypes of *A. ostoyae* and *A. luteobubalina*, respectively, may develop large, discrete, clones (2-3 ha or more) with individual genotypes occurring hundreds of meters apart (Adams 1974, Anderson and others 1979, Hood and Morrison 1984, Kile 1983b, Shaw and Roth 1976) (fig. 8.8). The size of some clones and the discontinuous distribution of some genotypes when compared with rates of spread is taken as evidence that the original infections may have begun decades or even several centuries previously (Kile 1983b, Shaw and Roth 1976). In contrast, *A. borealis*, *A. ostoyae*, *A. gallica*, *A. cepistipes*, *A. mellea*, *A. hinnulea*, *A. limonea*, and *A. novae-zelandiae* form relatively small clones (approx. 50-100 m maximum distance between isolates of the same genotype) in a variety of coniferous and moist temperate hardwood forests. A relatively frequent number of genotypes occurs per unit area, often in close proximity or intermingling and possibly with clones of more than one species (Hood and Sandberg 1987, Kile 1986, Korhonen 1978, McDonald and Martin 1988, Rishbeth 1978b, Thompson 1984, Ullrich and Anderson 1978).

Once established in the forest, any given genotype may persist for decades or centuries, occupying successive woody substrates as a result of parasitic and saprophytic activity. Multiple genotypes form a type of subterranean mosaic, but the physical and biochemical interaction between intra- or inter-specific genotypes has received limited investigation (Mohammed and Guillaumin 1989). These kinds of interactions could be mediated by extracellular structures such as those observed in *Postia placenta* (Fr.) M. Lars. et Lomb. (Green and others 1989), although they have not been observed in *Armillaria*.

Studies of dispersal and distribution emphasize the dynamic nature of the interaction between *Armillaria* species and natural forest ecosystems. Kile (1983b)

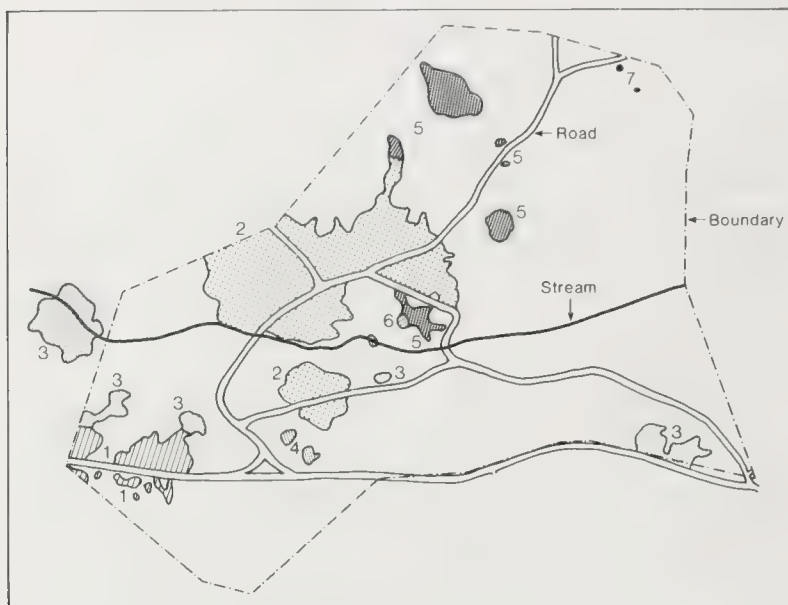


FIGURE 8.8 — Occurrence of seven genotypes of *Armillaria luteobubalina* in a eucalypt forest in the 33 ha Victoria Mill Scenic Reserve, Mount Cole State Forest, Victoria, Australia. (From Kile 1983b, courtesy Australian Journal of Botany)

considered that the major factors influencing clonal development were likely to be: the number and location of existing and new infections, the pathogenicity of the individual genotypes, their longevity in individual food bases, the stand and tree characteristics including host resistance, and perturbations within the forest such as fire and logging. Combinations of such factors over long periods could account for the limited size of some clones, the extensive or dispersed distribution of others, the presence of multiple genotypes in the same area, contraction or expansion of clone size, differing disease intensity, and predictably the loss of some genotypes from the forest.

Pathogenicity, Environment, Host Resistance, and Primary Disease Expression

As in other plant diseases, the expression of *Armillaria* root disease is influenced by species pathogenicity, host resistance, and environmental factors. How these factors interact relative to primary disease in natural forests is poorly understood at the present time.

A general observation can be made from the disease reports considered in this chapter: while non-lethal primary disease may be common in relatively wetter boreal and temperate forests (which may be translated into lethal secondary infection by stress), the most serious primary disease occurs in relatively drier Mediterranean or continental forests. As there is no evidence that recent introductions of pathogenic species are responsible for disease, the current situation presum-

ably reflects the results of long-term coevolution of hosts and pathogens.

One explanation for a difference of this nature in disease epidemiology encompasses the pathogenicity of the indigenous *Armillaria* species and the environmental and biological factors which control the population of the fungus. The large food base which may develop in wet forests in mild climates is seemingly balanced by the weak pathogenicity of the resident *Armillaria* species. In harsher forest environments, stress may have selected species or genotypes of greater pathogenicity which can effectively maintain themselves in the forest community from a more limited food base. In the former forests, weak pathogenicity, wide distribution, and long survival in inoculum are the elements of mutual coexistence (a feature of K-selected organisms). In the latter forests, greater pathogenicity, discontinuous distributions, and shorter survival in inoculum achieve the same end. In neither situation is the survival of the host species threatened. When stress leads to secondary *Armillaria* infection, not all trees are killed and such events typically lead to the establishment of regeneration.

These concepts, represented in fig. 8.9, can be illustrated by Australian examples. In Tasmania's wet sclerophyll eucalypt forest, *A. hinnulea* / *A. novae-zelandiae* are almost ubiquitous on root systems as epiphytic rhizomorphs or root lesions (Kile 1980b, Kile and Watling 1983). Logging or wildfire creates a vast food base and results in a high incidence of massive root and stump infection but with virtually no mortality among the regenerating stand of eucalypts and other species. Disease is restricted to the same form as that in the pre-existing stand (Kile 1980b). In Victoria's dry sclerophyll forest, on the other hand, eucalypts and other species are killed by *A. luteobubalina* even in the absence of artificial disturbance (Kile 1981, 1983b). However, food bases are fewer and the fungus generally only survives in stumps for 15-25 years (Kile 1981).

The relative pathogenicity of different *Armillaria* species on the same host under controlled conditions can be ranked (Morrison 1989). Variable disease expression on the same host supports the view that the differences described for eucalypt forests are to a significant degree caused by interspecific differences in pathogenicity rather than by host or short-term environmental effects. Messmate stringybark is a common host in both forest types, yet is only killed where *A. luteobubalina* occurs (Kile 1980b, 1981). Direct pathogenicity comparisons of the three *Armillaria* species present in the forests have not been made on messmate stringybark, but those tests undertaken with the individual species support the view that *A. luteobubalina* is inherently more pathogenic than either *A. hinnulea* or *A. novae-*

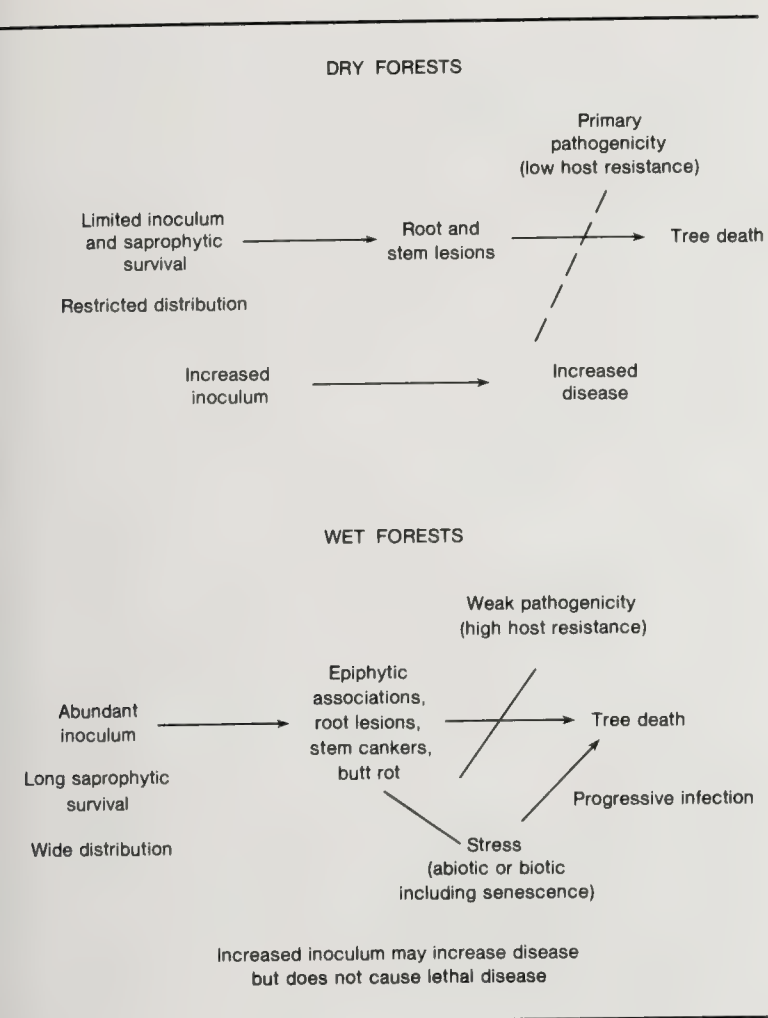


FIGURE 8.9—Conceptual models of the pathogenic behavior of *Armillaria* species in terms of two general forest environments.

zelandiae (Kile 1980b, 1981; Morrison 1989; Podger and others 1978).

Intra-regional differences in the epidemiology of disease caused by the same *Armillaria* species on the same or related hosts have been observed. In western North America, *A. ostoyae* is an aggressive pathogen on interior forest species but usually only causes minor disease on many of the same hosts in wet coastal forests (Morrison 1981, Morrison and others 1985a, Wargo and Shaw 1985). A similar situation may occur with *A. luteobubalina* in Western Australian forests. Shearer and Tippet (1988) noted that host mortality following infection was greater in the intermediate and low rainfall zones of the eastern jarrah forest than in the higher rainfall zones to the west. The fungus also appears to be less damaging in the wetter karri forest in the same region (Pearce and others 1986).

For western North America, Morrison and others (1985a) considered these differences might result from intraspecific variation in pathogenicity between coastal and interior isolates of *A. ostoyae*. McDonald and others (1987a,b) proposed that the difference in pathogenic behavior is linked to site productivity, host adaptation, or stress, with the incidence of pathogenic behavior

showing a strong tendency to decrease as stand productivity increased (fig. 8.9). They further suggested that disease incidence is also greatest in host populations in transition zones between climax species. These are seen as being less adapted to the site and therefore more vulnerable through lower host resistance. Soil factors may also be influential (Shields and Hobbs 1979, Williams and Marsden 1982). Intraspecific variation in host resistance has not been investigated relative to primary disease but could help explain regional differences in intraspecific pathogenicity. Presently, there is little basis on which to judge the merits of these different hypotheses, but they lend themselves to creative experimentation.

Possible feedback mechanisms such as that proposed for mountain hemlock stands infected by *Phellinus weirii* may also operate to influence host resistance during stand development. Waring and others (1987) suggested pathogen-induced disturbance may increase nutrient and light availability following death of mature stands, and increase resistance of young trees against infection. Although Shaw and others (1988) challenged this assumption and suggested vigorously growing young trees would have more roots and thus an increased probability of infection, such controversy does not deny the possible existence of such effects.

Disease expression in natural forests is clearly a complex phenomenon. Establishing the significance of host, pathogen, and environmental moderation in disease expression is a major challenge for future research. These interactions and consequent disease expression are in turn modified by forest management practices.

Forest Management and Disease

Forest harvesting and other disturbances cause fluctuations in inoculum levels in natural forests (Kile 1980b). In forests where the major *Armillaria* disease effects are non-lethal (root lesions, minor root rot, and butt rot), these fluctuations appear to have little effect on disease epidemiology from crop to crop unless management severely stresses residual trees. Where *Armillaria* species are aggressive primary pathogens, such as in the situations already described, management practices such as logging and control of fire severity and frequency may significantly affect disease expression. These may occur directly through impact on inoculum levels or interactions with species composition and stand structure. Much of the available information is observational, however, and little experimental study has been done on the effect of management practice on disease levels.

Selective logging in old-growth or mature-regrowth stands may intensify disease development in the re-

sidual stand. Damage is dependent on stand age and species and is usually attributed to increased inoculum, but physiological stress from exposure in retained trees could also be of some importance in increased tree susceptibility (see chapter 7). Logging old-growth ponderosa pine in southern Washington State led to striking disease development in young trees, with zones of dead and dying seedlings and saplings surrounding the infected old-growth stumps and eventually leading to the creation of an open area (Shaw 1975, Shaw and others 1976a). Harvesting, particularly selective logging, has also led to inoculum buildup on many species of conifer stumps in other western North American forests (Byler and others 1990, Filip and Goheen 1982, Hagle and Goheen 1988). Severe *Armillaria* root disease in dry sclerophyll eucalypt forest in Victoria, Australia was associated with repeated (approximately 10-year) selection cutting of the larger trees (Edgar and others 1976). Subsequently, Kellas and others (1987) showed that cutting intensity per se did not affect disease incidence, but that frequency of cutting within infected forests is probably the critical factor promoting disease development. Regular creation of stumps increased inoculum levels and the probability of residual trees being in close proximity to inoculum, thereby altering the balance in favor of the pathogen. Unless *A. luteobubalina* can access and infect stumps within 3-4 years of cutting, it is excluded from colonization by other microorganisms (Kile 1981). Clearfelling in disease patches could therefore be a better management practice by reducing the number of stumps infected and the disease level in the subsequent crop.

Partial cutting practices may make stands more susceptible to disease through changes in species composition. Selective logging in mixed-conifer forests in western North America, particularly those where species of pine and larch predominate, can favor regeneration of the more root-disease-susceptible Douglas-fir and true fir (Byler and others 1990, Filip and Goheen 1982, Hadfield 1984, Hagle and Goheen 1988, Shaw and others 1976a). Such changes may not always be adverse, however. Shelterwood cutting in dry sclerophyll eucalypt forest favors regeneration by broad-leaved and narrow-leaved peppermint as opposed to messmate stringybark, the commercially preferred species (Kellas and others 1987). The former species have a similar susceptibility to *A. luteobubalina*.

It may be feasible to space or commercially thin young, even-aged regrowth stands without increasing levels of *Armillaria* root disease if small stumps do not provide a sufficient food base to establish new disease foci, or tree vigor is enhanced sufficiently to resist root disease. Filip and others (1989) and Johnson and Thompson (1975) found no adverse effects on stocking 20 years after thinning in a young ponderosa pine stand, and

although Koenigs (1969) found thinning in an 80-year-old released understory stand of western redcedar increased root rot, disease was also apparently influenced by other stress factors. Precommercial thinning is generally not recommended in *Armillaria*-infected Douglas-fir regeneration (Morrison 1981). Further experimental studies on effects of spacing and thinning in relation to species composition appear necessary, however, before firm conclusions can be made.

Fire management can influence the susceptibility of forest stands to disease. Fire may directly affect *Armillaria* activity in forests through destruction of inoculum or indirectly through stress effects on the fungal mycelium which lead to natural biocontrol (Reaves and others 1990). Although a reduction in disease has not been demonstrated, fire frequency and intensity may also be a major determinant of the susceptibility of stands to disease through its influence on tree vigor, species composition, and stand structure.

No known studies quantify the effect of fire on inoculum quantity and viability, although Hood and Sandberg (1989) reported reduced isolation success from rhizomorphs on a clearcut native forest site after burning. General observations suggest a significant direct effect on inoculum levels is only achieved by high-intensity fire which burns or chars stumps and major buttress and lateral roots (Kile 1980b, 1981). Even then it is likely a significant proportion of below-ground inoculum will escape direct effects.

Munnecke and others (1976) showed that heating severely weakens the vitality of *Armillaria* mycelium, rendering it susceptible to parasitism by *Trichoderma viride* Pers.:Fr. and other soil-inhabiting fungi. Similar effects may operate to reduce inoculum in burned forests. Reaves and others (1990) found isolates of *Trichoderma* species from burned and non-burned soils beneath a ponderosa pine forest in Oregon were antagonistic to *A. ostoyae*, reducing colony growth and rhizomorph formation in culture. Isolates from burned soils were more antagonistic than those from non-burned soils as fire favored the growth of more antagonistic *Trichoderma* species. In the same situation, ash leachates inhibited growth of *A. ostoyae* in vitro while having a positive effect on *Trichoderma* (Reaves and others 1984, 1990). While appropriate use of fire may be effective in elevating populations of *Trichoderma* that are antagonistic to *Armillaria*, the mechanism, extent, and persistence of such effects need clarification.

In forest types in which burning has been a determinant of species composition and stand characteristics, fire suppression or exclusion may interact with silvicultural management to promote *Armillaria* root disease by allowing regeneration of species which are more

susceptible to *Armillaria* (Byler 1984, Byler and others 1990, Filip and Goheen 1982, Hagle and Goheen 1988, Shaw and others 1976a). Fire control associated with selective logging in drier coniferous forests in western North America has favored regeneration and overstocking of Douglas-fir and true fir in stands formerly composed predominantly of ponderosa and white pine and western larch, species apparently less susceptible or more tolerant to root disease. A need exists for more careful consideration of long-term ecological effects induced by various stand treatments on *Armillaria* root disease. A better understanding of such effects could lead to refinement of silvicultural methods.

While not a direct management effect, introduction of white pine blister rust (*Cronartium ribicola* J.C. Fisch.) into the northern Rocky Mountains of western North America has likely enhanced *Armillaria*-caused mortality (Byler and others 1990). The rust epidemic emulated a partial cut by killing large numbers of pole-sized and larger western white pines in many individual stands. It also modified succession in new stands by reducing or eliminating western white pine regeneration. A dramatic shift in species composition of many stands from the tolerant western white pine to susceptible Douglas-fir and grand fir was one result. The rapid killing of larger trees probably contributed to inoculum buildup as well. A related problem was the application of many western white pine salvage cuts due solely to the threat of *C. ribicola*.

Apart from direct management effects on quantity of inoculum or species composition, practices which severely stress plants may also increase disease. *Armillaria* species are thus a potential hazard for intensively managed coppice forests. Incidence and extent of root rot increased with shortened rotation in quaking aspen and bigtooth aspen sucker stands in Ontario and Wisconsin, and sucker numbers declined as a greater proportion of stumps were invaded by the fungus in successive rotations (Stanosz and Patton 1987a,b; Stiell and Berry 1986). Chronic low-level primary disease in the natural forest was transformed into more progressive secondary infection of physiologically stressed stumps and root systems by this type of management system.

Conclusions

Armillaria species are remarkably successful components of many natural forests. A large proportion of tree and shrub species of different strata, particularly in boreal and temperate forests, may be susceptible to *Armillaria* infection. Besides a pathogenic role, members of the genus contribute significantly to decomposition and mineral cycling as well as playing minor roles as mycoparasites and mycotrophic associates with some achlorophyllous plants.

Armillaria in natural forests is endemic, evidence of disease is often obscure, and it may often have minimal effect on host health and growth. However, a continuum of disease effects from non-lethal to lethal involves *Armillaria* species as primary or secondary pathogens. Epidemic disease involving *Armillaria* in either role may result when the balance between pathogenicity and host resistance is altered by stress or disturbance. Many forests may be utilized without aggravating the endemic disease level. In others, disturbance such as logging may lead to a major imbalance between host and pathogen. Inappropriate management in some regions has created a heritage of root disease problems.

Our understanding of the ecology and dynamic behavior of *Armillaria* in natural forests has developed significantly in recent years through better knowledge of species identity, pathogenicity, ecology, and a clear recognition of primary and secondary modes of behavior. In one case at least, it is now feasible to integrate this knowledge through a computer simulation model to better understand root disease dynamics and their response to forest management treatments (see chapter 10). Significant research needs remain. Specifically, future investigations should examine inoculum buildup, quantifying pathogen spatial distributions and dynamics, the relative importance of host, pathogen, and environment on disease expression, and the ecological effects of disease.

Armillaria in Planted Hosts

Ian A. Hood, Derek B. Redfern, and Glen A. Kile

In chapter 8, *Armillaria* was examined in its natural forest environment, modified or not by the activities of man. We now look at the disease in the various artificial habitats created when selected hosts are cultivated either for commercial production or as ornamentals for their aesthetic appeal. The distinction between natural and artificial environments is not always a sharp one, as when seedlings are planted beneath a natural overstory or when new plantations are infiltrated by seed regeneration from nearby stands. Indeed, it is sometimes difficult to decide if a plant growing within (or even outside) its natural range has been planted or naturally seeded. Even so, the planted host generally occurs in a very different setting from its natural counterpart which is adapted to its own particular ecosystem. We might therefore expect *Armillaria* to be frequent and widespread in many species of cultivated plants (Day 1929, Garrett 1956a, Mallet and others 1985).

To demonstrate just how widespread attack by *Armillaria* really is, a broad overview of the disease's geographic distribution begins the chapter. Sixty years of records are used to assess the global importance of *Armillaria* on cultivated plants. An account of the development and impact of *Armillaria* in plantations then follows, and the chapter is concluded by discussing how various management procedures may affect disease development.

Distribution and Importance

The literature on *Armillaria* in planted crops and ornamentals is vast. A large selection of reports has been collated and summarized in tables 9.1 (p. 140) and 9.2 (p. 142), and in fig. 9.1. Together, these present a broad picture of the disease in various host groups throughout the world (for host species lists see, for instance, Spaulding 1961, Raabe 1962a, Hansbrough 1964, Browne 1968). The number of references in these tables indicates the importance of the disease for particular hosts in different countries, with some qualifications: the number of references may reflect the regional activity of plant pa-

thologists besides that of the disease, and may be biased toward hosts of greater economic importance. The tables indicate only the presence of the disease, not its severity, which is often expressed only in qualitative terms. Despite these drawbacks, the figure and tables summarize where *Armillaria* occurs in planted hosts throughout the world.

Several trends may be detected in tables 9.1 and 9.2, and fig. 9.1. For example, *Armillaria* is not listed on any major cereals (wheat, rice, maize, oats, barley, rye) or certain other cultivated food crops (peas, beans, groundnut) which are normally cultivated on arable land but rarely, if ever, planted on former forest sites (see later). Records appear weighted in favor of cash-crop plants present in commercial plantations rather than non-commercial hosts used in subsistence cropping or shifting agriculture on cleared forest land. Records for ornamental trees and shrubs also seem under-represented and somewhat fragmentary. Probably many occurrences of the disease in amenity plantings go unreported or are listed only in unpublished records of state agricultural agencies and experiment stations.

Figure 9.1 clearly shows that *Armillaria* is widespread in planted hosts throughout temperate regions and in much of the tropics. Detailed information on disease occurrence in particular regions is normally unavailable but occasionally does exist. For instance, figure 9.2 shows the distribution of 574 *Armillaria*-caused deaths of mainly planted hosts in southern Britain during the past 25 years. Although the frequency of records is biased toward the collection center, and is influenced by the uneven distribution of parks or gardens and former woodland sites, results indicate a widespread occurrence of disease within the survey region. No doubt intensive long-term surveys would present a similar picture where conditions favor the disease elsewhere in the world (Hood 1989).

Lack of detailed information on disease incidence prevents precise comparisons between regions. However,



FIGURE 9.1 — Distribution of recorded *Armillaria* attacks in planted hosts, by country (and region).

the literature suggests that the disease is most common in areas with a moist environment and a moderate temperature range (Bliss 1946; Browne 1968; Bunting 1924; Fox 1964; Gibson 1961, 1975, 1979; Ivory 1987; Jie 1982; Jorge 1977; Kile 1980a; Longenecker and others 1975; Mańka 1980; Mohammed and others 1989; Rivera 1940; Rudd-Jones 1950; Rykowski 1980; Sokolov 1971; Tarry 1969). Precipitation and temperature may be the primary factors governing both the altitudinal and latitudinal distributions of *Armillaria*. Thus, in many tropical areas the disease is known only in plantations established at higher elevations where the climate is cooler and wetter (Arentz and Simpson 1989, Barnard and Beveridge 1957, Bernard 1926, Brazilian Inst. Forestry Dev. 1976, Fox 1970, Gill 1963, Ivory 1975, Raabe and Trujillo 1963, Rayner 1959, Satyanarayana and others 1982, van der Goot 1937). This contrasts with certain other tropical root disease fungi which are found mainly in plantations growing at low and mid elevations where the climate is hotter (*Phellinus noxius* (Corner) Cunningham, *Rigidoporus lignosus* (Klotzsh) Imazeki, Fox 1970). In the temperate zones, *Armillaria* attacks plantations established at low and mid altitudes, but not those planted at higher elevations where it is too cold (Johnson 1976, Rahm 1956, Singh and Khan 1979, Twarowski

and Twarowska 1959). In the same way, the disease may occur less often at higher latitudes where the climate is colder. *Armillaria* also appears to be absent from certain inland regions with extreme continental climates, as in parts of the Soviet Union (Sokolov 1964).

Europe and the Soviet Union

Europe has a tradition of plantation forestry dating back at least 3 centuries. *Armillaria* is widespread in forest plantations on this continent, and few countries, if any, lack disease records (tables 9.1, 9.2a,b; Day 1929; fig. 9.1). Reports are particularly numerous from France (see also Boullard 1961), Germany, Poland, and the United Kingdom. *Armillaria* is widespread in planted forests in the Soviet Union, (Fedorov and Bobko 1989, Fedorov and Poleschuk 1981, Fedorov and Smoljak 1989, Sokolov 1964) and has also been found on eucalypt species in Spain, Portugal, and Cyprus (Gibson 1975, Ivory 1987). Reports are more numerous for conifer than hardwood stands (tables 9.1, 9.2a).

Much fundamental research has been undertaken in European plantations since Robert Hartig first established the relationship between *Armillaria* and disease



FIGURE 9.2 — Distribution of deaths in planted hosts due to *Armillaria* in southern Britain, 1962-1986. Dot diameter indicates number of records (respectively, over 50, 20-50, 10-20, under 10, in decreasing order of size; data courtesy Pathology Branch Advisory Service, UK Forestry Commission).

in Germany in 1873 (Hartig 1873b, 1874; Nechleba 1915), and this has contributed greatly to our knowledge of the disease's nature and development worldwide. Until recently, most disease records in Europe were attributed to *A. mellea* (*sensu lato*), and sometimes *A. tabescens*. We now know (see chapters 1, 2) that attack in European plantations is caused predominantly by *A. mellea* (*sensu stricto*) and *A. ostoyae* (Korhonen 1978, reviewed Roll-Hansen 1985). This knowledge has encouraged research to define the ecological roles and behavior of the European *Armillaria* species (Guillaumin and Berthelay 1981; Guillaumin and Lung 1985; Guillaumin and others 1984, 1985, 1989a; Holdenrieder 1986; Rishbeth 1982, 1983, 1985a,b, 1987; Siepmann 1985). Recent work shows that at least in western Europe vigorous trees in pure conifer plantations are attacked mainly by *A. ostoyae*. Most infection in planted hardwoods (forest and ornamental trees, table 9.2a) is due to *A. mellea*; in stressed hosts, several less pathogenic species are sometimes responsible (e.g., *A. gallica*; Clancy and Lacey 1986; Davidson and Rishbeth 1988; Durrieu and others 1985; Guyon and others 1985; Intini 1989a,b; Laville and Vogel 1984; Lung-Escarmant and Taxis 1985, 1989). More severe attacks in conifers usually occur on former natural hardwood forest sites (often oak) rather than pure conifer stands (Peace 1962, Redfern 1975, Rishbeth 1982, Ušćuplić 1980), so that the precise manner in which *A. ostoyae* invades and develops in new conifer plantations requires elucidation (Guillaumin and others 1989a). Guillaumin and Lung (1985) indicated, however, that *A. ostoyae* can grow and produce rhizomorphs quite successfully on hardwood

species even though it is a parasite primarily on conifers (see also Davidson and Rishbeth 1988, Gregory 1989, Redfern 1975, Rishbeth 1982).

Although *Armillaria* is considered Europe's most important root disease after *Heterobasidion annosum* (Fr.) Bref., its impact on forest plantations is comparatively minor in this region (Peace 1962). It creates canopy gaps and lessens the returns from early thinnings; but in general, the effects of early mortality are probably over-estimated due to the rather spectacular appearance of the disease in young stands (Pegler and Gibson 1972). Under certain stand or site conditions, damage can become more severe on some hosts. For instance, in Poland *Armillaria* has been responsible for serious losses of Norway spruce and Scots pine (Mańka 1980, 1981; Twarowski and Twarowska 1959; table 9.1).

Armillaria kills ornamental trees and shrubs planted in gardens, parks, and reserves (table 9.2b; Ingelström 1938) and reports are particularly numerous from Great Britain (Boughey 1938, Gibbs and Greig 1990, Greig and Strouts 1983, Peace 1962, Rishbeth 1983, Schilling 1989). The records of mortality shown in fig. 9.2 were predominantly from amenity plantings and were mainly on hosts in the families Pinaceae (31% of records), Rosaceae (21%), Fagaceae (13%), Oleaceae (12%), and Salicaceae (10%).

Food production is far older than plantation forestry, and losses from *Armillaria* must have occurred historically wherever people cultivated plants. Today, the disease commonly attacks many European crops, particularly pip fruit (*Citrus*, Mediterranean countries), pome fruit (*Malus*, *Pyrus*), stone fruit (*Prunus*, Guillaumin 1977, Guillaumin and Pierson 1983, fig. 9.3), walnuts, and grapes (Guillaumin 1986b, see table 9.2b and Guillaumin 1982, Guillaumin and others 1982, fig. 9.4a). The



FIGURE 9.3 — Mortality gap in almond orchard (on peach rootstock) caused by *A. mellea* with trees dying at the margin; Aigaliers, southern France. (D. Barrett)



A



B

FIGURE 9.4 — A: Mortality gap in grape vineyard, caused by *A. mellea* near Bordeaux, France. (J.-J. Guillaumin). B: Group of trees killed by *Armillaria* sp. in 15-year-old plantation of slash pine; Usa, Tanzania. (M.H. Ivory)

disease has been reported less frequently in cane fruits (Marsh 1952), cork oak, fig, and flower crops (Guillaumin and others 1982), hazelnut, hops, kiwifruit, mulberry, olive, strawberry, various vegetable crops, and in an *Opuntia* cactus crop (grown for its edible fruits). *Armillaria* also attacks various cultivated crops in

Lithuania and the Ukraine (Dist. of Plant Dis. 1980), and in Azerbaijan, Armenia, Georgia, Belorussia, Tatar, and eastern Kazakhstan (Sokolov 1964).

Details of *Armillaria* in European plantations have been reviewed by Peace (1962), Pawsey (1973), Schönhar (1977), Rykowski (1980), Guillaumin (1982, 1988), Guillaumin and others (1982), Roll-Hansen (1985), and Phillips (1988). Greig and Strouts (1983) give a popular account of the disease in Britain.

North America

The behavior of *Armillaria* in both managed and unmanaged forests has been extensively researched in North America since early this century (Byler 1984, see chapter 8). In many of these stands, *Armillaria* occurs as an important butt-rot agent and also influences forest successional development by killing seedlings, saplings, and more mature trees, particularly those already weakened by other causes (Byler 1984; Wargo 1980b, 1984b). Most reports of disease in forest plantings are from coniferous stands (table 9.1). Records on hardwoods have come mainly from ornamental or shade trees in the eastern half of the continent (table 9.2a). In conifer plantations in the west, *Armillaria* is one of several important root- and butt-rot disease fungi such as *Phellinus weirii* (Murr.) Gilb. and *H. annosum*, which often occur in the same host or stand. Until recently, all North American records of *Armillaria* were attributed to *A. mellea* (or *A. tabescens*, see below). At least nine biological species of *Armillaria* are now known on the continent, some of which are related to European species (see chapters 1, 2). As in Europe, work is currently underway to define the ecological roles of these species and to identify those which cause disease in plantations and managed stands (Mallet and Hiratsuka 1988, McDonald and Martin 1988, Proffer and others 1987).

Present forests in western North America originated largely by natural seeding following logging of the old growth forests that began during the 19th century. Planting is now carried out to improve stocking levels of desirable species. Early *Armillaria* research in planted forests was done in coastal British Columbia, where trees in young plantations of Douglas-fir are killed by a species now identified as *A. ostoyae* (Bloomberg 1990; Buckland 1953; Hood and Morrison 1984; Johnson and others 1972; Morrison and others 1985a,b; Pielou and Foster 1962). Morrison (1981) reviewed the current understanding of the disease in this province. He considered *Armillaria* to be comparatively unimportant in coastal conifer plantations because mortality is low (1-5%), and ceases after about age 25 years. By contrast, interior British Columbia experiences higher mortality in both plantations and natural, mixed conifer forests (Bloomberg and Morrison 1989; Morrison 1981; Morri-

son and others 1988). In neighboring Alberta and other prairie provinces of Canada, disease impact has not been great, and mortality from *Armillaria* has occurred mainly in naturally regenerated conifers (Blenis and others 1987, Hiratsuka 1987, Mallet 1989). However, deaths also occur in plantations (Emond and Cerezke 1990, Hiratsuka 1987), and *Armillaria* root disease may become more common as management intensifies (Blenis and others 1987). Preliminary work suggests that the species pathogenic to conifers in Alberta are *A. ostoyae*, a form of *A. cepistipes*, and possibly *A. mellea* (Blenis and others 1987, Mallet 1989, Mallet and Hiratsuka 1988). In Europe, *A. cepistipes* is not considered to be a serious parasite (see chapter 6), and *A. mellea* is most important on hardwood hosts (Davidson and Rishbeth 1988, Guillaumin and others 1989a).

Armillaria root disease (apparently *A. ostoyae*, Filip 1989a, Hadfield and others 1986, Morrison and others 1989) is widespread in western Washington and Oregon, but has the same low impact in conifer plantations as it has in adjacent coastal British Columbia (Filip 1979, Hadfield and others 1986, Johnson 1976). The disease also affects ornamental plants in urban areas in this region (Schmitz 1920). *Armillaria* kills planted ponderosa pine in central Oregon (Adams 1974), but at present it has greater impact in managed natural stands of ponderosa pine and other species in central and eastern Oregon and Washington (Hadfield and others 1986, see chapter 8).

Armillaria is of little consequence in planted and natural coniferous forests in California (table 9.1), but it does attack many ornamental, orchard, and horticultural host species in this State (tables 9.2a,b; see below), suggesting that perhaps different species are involved (Adaskaveg and Ogawa 1990). Although *Armillaria* occurs in conifer plantations in Idaho and New Mexico (Weiss and Rifle 1971, table 9.1), the disease has only been reported from natural forests in Montana, Wyoming, Utah, and Colorado (Wargo and Shaw 1985). *Armillaria* is found across parts of the Great Plains, including North and South Dakota, Nebraska, Kansas, Oklahoma, and the eastern edges of Montana, Wyoming, and Colorado, where it occurs sporadically in over 25 tree species established as windbreaks, Christmas tree, recreational, roadside, and landscape plantings (Fuller and James 1986). The species identification is unknown.

Armillaria is present in Canada's eastern maritime Provinces and has caused disease in planted conifers in Quebec (table 9.1, Magasi 1990). In Newfoundland, it causes serious disease in plantations of native and introduced species of fir, spruce, and pine (Hall and Schooley 1981; Hall and others 1971; Khalil 1977; Singh 1978, 1980a,b, 1981b,c, 1983; Singh and Bhure 1974;

Singh and Richardson 1973). Losses may exceed 30% but are usually lower. The disease also affects urban and shade trees in Newfoundland (Singh and Carew 1983). In Ontario, *Armillaria* frequently infects both natural forests (Basham 1958, Hord and Quirque 1956, Whitney and MacDonald 1985) and conifer plantations (Huntley and others 1961; Whitney 1983, 1988b; Whitney and others 1978, 1989a). Losses have not been serious, in some cases because trees were established on abandoned farmland. The species pathogenic to conifers in this province is *A. ostoyae* (Anon. 1989, Whitney and others 1989a). *Armillaria* is also present in Manitoba's forest plantations (C.G. Shaw III, pers. comm.).

Across the southern border, the disease attacks conifer plantations in Minnesota (9% mortality; Livingston and others 1982), throughout Wisconsin (Patton and Riker 1959), and in Michigan (under 5%; Bruhn and others 1989). Several planted stands of red pine in Wisconsin experienced mortality ranging from 10% to 37% at age 10 years after the natural oak overstory was killed by aerial application of herbicide (Pronos 1977; Pronos and Patton 1977, 1978). Although few reports document *Armillaria* in planted hosts in the northeastern USA, the disease is common there and causes losses in forests and Christmas tree plantations (table 9.1, Cook 1961, Longenecker and others 1975, Silverborg and Gilbertson 1962). Ornamental and urban shade trees are also attacked, and *A. mellea* and *A. gallica* both occur on hardwoods in this region (Dunbar and Stephens 1975, Motta and Korhonen 1986). *Armillaria* has little impact in eastern white pine plantations in North Carolina (Leininger and others 1970).

In the southern and southeastern USA (Mississippi, Louisiana, Georgia, Florida) *Armillaria* attacks many different ornamental and shade trees (table 9.2a; Rhoads 1956, Sinclair and others 1987). It and other fungi have reportedly caused up to 25% mortality in plantations of sand pine (Barnard and others 1985, Ross 1970). The pathogen in this region was known as *Clitocybe tabescens* as early as 1930 (table 9.2a), and the disease is still attributed to *A. tabescens* in current reports (Sinclair and others 1987) although further examination is needed to establish its identity (Guillaumin and others 1989a).

For reviews of *Armillaria* in North American forests, including plantations, see Boyce (1938), Singh (1980b), Wargo and Shaw (1985), and Sinclair and others (1987). Hepting (1971) supplied information for individual hosts, and a popular account of the disease was recently prepared by Williams and others (1989).

Armillaria severely affects orchard and horticultural crops in North America, particularly in California, Florida, and the Pacific Northwest (Washington, Ore-

gon, and British Columbia). In California, it is considered one of the most serious diseases of stone fruits (Wilson and Ogawa 1979), and it also infects citrus, walnuts, and grapes (table 9.2b). The disease has affected these crops since the turn of the century on sites previously forested with native oaks, giving rise to the name “oak root fungus” (Gardner and Raabe 1963, Hewitt 1936). *Armillaria* infects California’s pome fruits (table 9.2b), but it is apparently unimportant in apple and pear orchards (Wilson and Ogawa 1979). The disease has also been recorded on California’s avocado, blackberry, fig, kiwifruit, loquat, persimmon, and strawberry crops (table 9.2b). Wilson and Ogawa (1979) included olive, chestnut, hazelnut, commom pistachio, and common pomegranate as additional hosts in the State.

In Washington and Oregon, hosts include currants, gooseberries, hazelnuts, hops, pome fruits, raspberries, stone fruits, strawberries, and walnuts (table 9.2b, Childs and Zeller 1929, Lawrence 1910, Piper and Fletcher 1903). *Armillaria* occurs in British Columbia’s pome and stone fruits, and occasionally its raspberries and potatoes (table 9.2b). In Florida, *Armillaria* (cited as “*A. tabescens*”) has been reported on citrus (Rhoads 1948), and stone fruit trees have been attacked in several southeastern States (table 9.2b; Weaver 1974). Other host crops in Florida have included banana, grape (also in Missouri), guava, litchi, pome fruits (also in Louisiana), and tung (also in Louisiana). Pecan trees have been attacked in Georgia, and stone fruit trees in Wisconsin, Illinois, Michigan, Ontario, and Quebec. The disease is recorded on fruit trees in the Eastern States of North Carolina and Maryland (Cooley 1943).

Little work has been done to identify which species of *Armillaria* attack horticultural and fruit crops in North America. In Michigan, Proffer and others (1987) found *A. ostoyae*, *A. mellea*, and a species since described as *A. calvescens* (Bérubé and Dessureault 1989) attacking sour cherry trees planted on susceptible root stocks (see also Adaskaveg and Ogawa 1990).

Central and South America

Records of disease on planted hosts are much less frequent from Central and South America, but they suggest that *Armillaria* has a wide, if sporadic, distribution in both the tropic and temperate zones throughout the region (table 9.1, 9.2a,b).

In warm-temperate, northern Mexico, *A. ostoyae* has caused root disease in radiata and Arizona pine plantations near Chihuahua (Hawksworth 1987, Shaw 1989a).

Armillaria occurs in tropical America and has been recorded on conifers in Jamaica and Peru, mainly on

pinus such as slash pine (table 9.1). According to Ivory (1987), pinus have been attacked in Cuba, Honduras, Surinam, and Ecuador. C.A. Garzon B. (pers. comm.) has observed mortality caused by *Armillaria* among planted eucalypts at high elevation near Popayán in western Colombia. The disease was reported in Colombia between 1975 and 1982 in slash pine, Mexican weeping pine, Mexican cypress, teak, and eucalypts (C. Alvarado, J.J. Castaño, M. Gutierrez, E.R. Ordoñez, M.; per C.A. Garzon B.), but it is not considered to be important in that country. One account documents *Armillaria* on hardwoods in Peru (table 9.2a), but it is not recorded in the extensive eucalypt, Gmelina, and pine plantations that have replaced natural rainforest in the Amazon Basin of Brazil, suggesting that the disease currently has little, if any, significance in the hot, low-land climate of this region (Brazilian Inst. Forestry Dev. 1976, Rankin 1985).

Few records implicate the disease among cultivated crops in tropical America. *Armillaria* has been reported on cacao in Mexico, Colombia, and possibly Brazil; and it is listed on avocado in Ecuador (table 9.2b; Wood and Lass 1985). Locally, *Armillaria* has infected Cinchona plantations in Peru (table 9.2b) and economic food crops in the Dominican Republic, Guatemala, and Surinam (Dist. of Plant Dis. 1980). However, it is not notable as a problem in cacao in Ecuador (J. Hedger, pers. comm.), and it was not detected in Trinidad and Venezuela (Dennis 1950, 1970). Nothing is known of the species responsible for disease in tropical America.

In temperate South America, *Armillaria* has been reported from Chile and southern Brazil on introduced conifers, especially pinus (table 9.1). The disease has killed groups of radiata pine less than 6 years old in Chile, but 1% or less of the forest is affected (H. Peredo L., pers. comm.). Reis (1974) noted that *Armillaria* had been recognized for a number of years in pine plantations in Chile (radiata pine) and Brazil (slash, loblolly, and Mexican weeping pine; May 1962a,b, 1964; Brazilian Inst. Forestry Dev. 1976). Gibson (1973) observed minor damage in slash pine plantations up to 12 years old near São Paulo. In its warmer, northerly range in southern Brazil, the disease is confined to higher elevations (Brazilian Inst. Forestry Dev. 1976). Mortality varies between 1% and, rarely, 25-30%, and ceases after age 5 years (Brazilian Inst. Forestry Dev. 1976, Ferreira 1989, Hodges 1971). Among cultivated plants, *Armillaria* has been reported on cassava and pome fruits in Chile and grapes in southern Brazil (table 9.2b; May 1962a). No published records of the disease so far exist for plantations in Argentina (J.E. Wright, pers. comm.).

Many *Armillaria* species have been described from temperate South America, including *A. limonea* and *A. novae-zelandiae* which are pathogenic in Australasia

(Horak 1979; Kile and Watling 1983; Shaw and Calderon 1977; Singer 1953, 1969; Spegazzini 1922), but the species causing disease in pine plantations and horticultural crops have not been identified. However, the Northern Hemisphere species are very likely absent or of only minor importance in the south-temperate regions of the world.

Africa

Africa has provided many records of *Armillaria* in various planted hosts from numerous localities (tables 9.1, 9.2a,b; Ivory 1988). These are scattered from the north-temperate zone (Morocco, Algeria, Tunisia, Libya) across the tropics to temperate southern Africa (fig. 9.1). The impact and intensity of disease varies with location and host. A number of reviews, surveys, and literature collations have been published (Browne 1968; Fox 1970; Gibson 1967, 1975, 1979; Ivory 1987; Mohammed and others 1989). According to Mohammed and others (1989; cf Mwangi and others 1989), the two most common species on planted hosts are *A. heimii*, which was collected mainly above 2,000 m in eastern, central, and southern Africa, and a species culturally close to *A. mellea* which was found at lower altitudes on both sides of the continent (Pegler 1977). Both occurred on hardwood and conifer plantation species and on horticultural crops. These distributions are interesting because *Armillaria* tends to infect plantations established above 1,000 m in eastern Africa where the climate is cooler and wetter. In central and west Africa (Ghana, Nigeria, Zaire, Uganda), the disease occurs in crops at both high and low altitudes (Blaha 1978, Fox 1970). Further surveys are needed, however, before the various altitudinal occurrences of disease on each side of the continent can be considered species-related.

Plantations of fast-growing hardwood and softwood trees have been established in many African countries in order to replenish natural timber resources that are gradually becoming exhausted (Gibson 1967; Ofosu-Asiedu 1980, 1988; Wingfield 1987). Losses from *Armillaria* have been recorded in species of *Araucaria*, *Pinus*, *Widdringtonia*, *Acacia*, *Albizia*, *Cassia*, *Cedrela*, *Cupressus*, *Eucalyptus*, *Gmelina*, *Grevillea*, *Khaya*, *Tectona*, *Terminalia*, *Toona*, and *Vitis* (Gibson 1967, 1975; L.M. Mwangi, pers. comm.; fig. 9.4b). Other reports supplementing those listed in table 9.1 and 9.2a are supplied by Gibson (1964, 1967, 1975); Scharif (1964); Browne (1968); Saccas (1975); Bakshi (1976); Ofosu-Asiedu (1980); Nandris and others (1984); Pearce (1976, 1984); Nicole and Mallet (1985); and Chipompha (1987). These document additional location records of the disease in planted forest species in Cameroon, Central African Republic, Gabon, Ivory Coast, Morocco, Nigeria, Sudan, Swaziland, and Zambia (fig. 9.1). In West African countries, incidence of disease is normally infrequent

and occurrence is confined to localized infection centers, but Gibson (1967) reported up to 60% loss of *Albizia falcata* in Gabon. In North Africa the disease has been reported from Tunisia (eucalypts, occasional deaths, Gibson 1967) and Morocco (teak, up to 20% losses on some sites from *Armillaria* and *Rigidoporus lignosus* (Kl.) Imaz, Gibson 1967).

Armillaria has been investigated intensively in forest plantations in Kenya, Malawi, and Zimbabwe (Chipompha 1987; Gibson 1957a,b, 1960, 1961; Gibson and Corbett 1964; Gibson and Goodchild 1960; Masuka 1989; Olembo 1972; Olembo and others 1971; Swift 1968, 1970, 1972). In these countries, attack occurs on cool, moist, higher sites formerly occupied by natural rain forest rich in hardwood species (Leach 1939) or on old hardwood plantation sites (Gibson 1979). Overall, the impact of the disease is minimal, but it can be locally severe (over 30% mortality) in younger stands of susceptible species such as teak, slash pine, and mlanji cedar. Normally of little or only local significance, *Armillaria* infects plantations of pine, teak, and occasionally other species in Uganda, Tanzania, Zambia, Swaziland, and South Africa (Gibson 1964, 1967, 1975; Kotzé 1935; Lückhoff 1964; Lundquist 1986, 1987; Lundquist and Baxter 1985; Pearce 1984; Wingfield 1987; Wingfield and Knox-Davies 1980; Wingfield and others 1989).

The horticultural crops most commonly attacked in tropical Africa (table 9.2b) have been cacao (countries bordering the Gulf of Guinea, Central African Republic, Zaire, Uganda and Madagascar; Saccas 1975), coffee (widespread; Guinea to Mauritius, Ethiopia to Zimbabwe; Blaha 1978), tea (central and east Africa from Zaire to Mauritius, Kenya to Zimbabwe; Fassi 1959; Leach 1937, 1939), and rubber (central Africa from Liberia to Uganda; Fox 1964, 1970; Mallet and others 1985; Wastie 1986; D. Nandris, pers. comm.). Brief reviews of the disease have been published for cacao (Thorold 1975, Wood and Lass 1985), and for tea and coffee (Haarer 1963, Saccas 1975, Wallace 1935). In tea and coffee, the disease is known as "collar crack disease."

Armillaria has been reported less frequently on the following cultivated hosts in Kenya, Uganda, Tanzania, Malawi, Zimbabwe (table 9.2b; Saccas 1975, Wiehe 1952): banana, cassava, Cinchona, citrus, fig, guava, geranium/pelargonium, granadilla, loquat, macadamia nut, mango, olive, papaya, pome fruit, stone fruit, sugar cane, and tung. Additional hosts in Zimbabwe are avocado, cotton, grapes, pecan, and strawberry (F.A. Chanakira-Nyahwa, pers. comm.). Records elsewhere in tropical Africa (table 9.2b; Saccas 1975, Turner 1970, Wardlaw 1965) include avocado (Ghana), banana (Ghana), cassava (Ivory Coast, Central African Republic,

Zaire), *Cinchona* (Guinea, Zaire), coconut (Ghana), *Cola acuminata* (Ghana), cotton (Zaire), *Hydnocarpus anthelmintica* (Zaire), lime (Ghana), mango (Ghana), mulberry (Central African Republic), oil palm (Ghana, Zaire), and pome fruit (Zaire). Wardlaw (1972) reviewed the disease in banana. Further records of *Armillaria* in cultivated plants are listed from Angola, and possibly Egypt and Sierra Leone (Dist. of Plant Dis. 1980). In temperate Africa, *Armillaria* has been recorded on fig and citrus in the north (Algeria, Libya, Morocco, Tunisia), and from banana, citrus, stone, and pome fruit trees in South Africa (Wingfield 1987).

A variety of tropical ornamental trees and shrubs are subject to attack from *Armillaria* in Zimbabwe (F.A. Chanakira-Nyahwa, pers. comm.), and the same is no doubt true of other countries in Africa.

Asia and the Pacific

Records of *Armillaria* in planted hosts are widespread, but sporadic, from the Middle East to the Pacific Ocean, even though parts of this region (China, Japan) have a centuries-old reforestation tradition (Izumi 1988, Winters 1974). In north temperate Asia, the disease has been reported in economic crops from Iran and apparently Iraq (Dist. of Plant Dis. 1980, Bakshi 1967) and in conifer plantations or hardwood trees from Pakistan, India, China, Korea, and Japan (table 9.1; Bakshi 1967). A record from cypress in Lebanon may refer to a plantation (Scharif 1964), and in northern Pakistan, infection has been observed on persimmon (Zakaullah and others 1987). *Armillaria* occurs in the western Himalaya Ranges in northern India (Bakshi 1976, 1977) but caused less than 3% mortality in young plantations of deodar cedar and pindrow fir (Singh and Khan 1979). Further east, *Armillaria* has been found in exotic pine and Japanese redcedar plantations in northern West Bengal (Bakshi 1976, Singh and Khan 1982).

Armillaria is widespread in China (Zhang and Huang 1990). Jie (1982) described extensive attack in Heilong-Jiang province in the northeast affecting plantations of Korean pine and larch. She reported *Armillaria* in the interior provinces of Gansu, Sichuan, and Yunnan, on both broadleaf and conifer hosts. *Armillaria* infects planted Korean pine trees but is not considered serious in Inner Mongolia province (Yang Li, pers. comm.). In Hebei province the disease is attributed to *A. tabescens* and is recorded in fruit, ornamental, and woodlot trees (apple, pear, peach, almond, white mulberry, locust, poplar, willow, elm, ailanthus, and jujube; Chang and others 1982). *Armillaria* is a serious problem on citrus in Sichuan province, and on tea and cocoa in Yunnan province in the south (Beijing Forestry University 1983).

Armillaria occurs throughout Japan and kills trees in young plantations of Japanese larch (Bakshi 1967; Imazeki 1964; Kawada and others 1962; Ono 1965, 1970) and hinoki (Muramoto 1987, 1988; Terashita and others 1983). Mortality rates for hinoki in Kagoshima Prefecture (Kyushu) are mostly under 10% (M. Muramoto, pers. comm.). *Armillaria* has been reported on pine in Japan (Bakshi 1976; Kitijima 1934). It also affected a cherry orchard near Osaka (Aoshima and Hayashi 1981). According to Guillaumin and others (1989a), *A. mellea* is one of the species commonly present in southern Japan where it occurs mainly on non-conifers although three isolates were obtained from hinoki. A Sakhalin spruce collection made from northern Japan was identified as *A. ostoyae*. This and other species have been reported from northern India (Chandra and Watling 1981, Watling and Gregory 1980), but generally more work is needed to clarify our knowledge of the pathogenic species inhabiting plantations in temperate Asia (see chapters 1 and 2).

Armillaria also infects coniferous and hardwood hosts in Korea (Bakshi 1967, Imazeki 1964, Lee and others 1987). The disease occurs in plantations of Korean pine (Sung and others 1989) and also mulberry plantations and orchards (Office of Forestry 1969).

In tropical Asia, reports of disease are few, and while this may reflect less disease research in some countries, *Armillaria* causes little or no impact in lowland areas over much of the region. It is rare in tropical India (Ivory 1988), but *Armillaria* has affected green wattle in the south (Nilgiris hills) and *Acacia* and *Albizia* in Sri Lanka (table 9.2a; Gibson 1975). Petch (1910, 1928) studied the disease in Sri Lankan tea plantations and found that stumps of interplanted *Acacia* species fostered disease spread. Tropical crops such as cacao, coffee, and tea are commonly cultivated beneath a canopy of quick-growing hardwood shade trees such as *Acacia*, *Casuarina*, *Gliricidia*, and *Leucaena* (Wood and Lass 1985). Generally, however, *Armillaria* has little impact in Sri Lanka and is not normally seen in horticultural crops there (A. de S. Liyanage, pers. comm.). *Armillaria* was reported on tea in southern India several times since 1960 (table 9.2b), but a record on tung has been disputed (table 9.2b). The pathogenic species in tropical India and Sri Lanka has been described as *A. fuscipes* which may be identical to or closely related to the African *A. heimii* (Chandra and Watling 1981, Kile and Watling 1988, Pegler 1986).

Armillaria has been recorded in Vietnamese (Dist. of Plant Dis. 1980) and Philippine crops (Saccas 1975, Mallet and others 1985, Dist. of Plant Dis. 1980). Reports concerning conifer hosts in the region are few, but *Armillaria* has caused low levels of disease in plant-

ings of Khasi pine and Bahaman pine in the Cameron Highlands of Peninsular Malaysia (Barnard and Beveridge 1957; Ivory 1972, 1975; M.H. Ivory, pers. comm.). In Indonesia, *Armillaria* (sometimes as *A. fuscipes*) was reported several times in the 1920's and 1930's in *Cinchona*, tea, coffee, and citrus in Sumatra and Java. These records were frequently at higher elevations. *Armillaria* has been found in planted hardwood tree species such as *Albizia*, *Leucaena*, green wattle, and teak in Java and Sulawesi (table 9.2a,b; Gibson 1975, Hadi 1977, Imazeki 1964), but the disease is not common in Indonesia today (S. Hadi, pers. comm.).

Records from Malaysia and Indonesia appear restricted to higher elevations, suggesting that *Armillaria* naturally inhabits the cooler, more temperate, montane forest types rather than lowland, tropical rainforests in this region (Fox 1970). In Peninsular Malaysia, *Armillaria* is absent from lowland plantations of rubber, oil palm, Caribbean pine, *Acacia mangium*, *Gmelina arborea*, and *Paraserianthes falcataria* (R.A. Fox; K.H. Chee; A.M. Tan; Lee S.S.; Norani Ahmad; Maziah Zakaria, pers. comms.).

In Papua New Guinea, too, *Armillaria* occurs only at mid or higher elevations where it causes root rot and mortality in planted pines and eucalypts (F. Arentz, pers. comm., Arentz and Simpson 1989, Shaw 1984). J.A. Simpson (pers. comm.) observed the disease in eucalypt plantations (swamp mahogany and southern blue gum) established mainly on certain sites cleared of natural southern-beech forest. Mexican weeping pine was also killed by *Armillaria* at Marafunga. Other eucalypt species (e.g., flooded and New Guinea gums) showed no evidence of disease on most sites, and infections in pines (Khasi, Mexican weeping, and Honduran at Lapegu and Kainantu) caused no economic loss. *Armillaria* has been recorded in Papua New Guinea on several cultivated crops such as coffee (Shaw 1984; table 9.2b), but is of little economic significance on these hosts. *Armillaria* collections made in Papua New Guinea have been identified as *A. mellea*, *A. fellea*, and *A. heimii* (Shaw 1984), and according to J.A. Simpson (pers. comm.), southern blue gum was attacked by *A. novae-zelandiae*, and swamp mahogany by *A. fellea*.

Few records document the disease in the tropical Pacific (Dingley and others 1981). *Armillaria* attacks Fiji's high- and low-elevation plantings of mahogany and slash pine on former rain forest sites (Singh 1978, Singh and Bola 1981; pers. obs.). It also occurs in the Solomon Islands (Corner, in McKenzie and Jackson 1986) but has not been reported in plantations. In Hawaii, *Armillaria* causes disease in young pine plantations over 1000 m elevation, and it also occurs in planted hardwood hosts (Laemmlen and Bega 1974, Raabe and Trujillo 1963).

The species responsible for the disease in these islands is unknown.

Australasia

Armillaria is of little consequence on planted hosts in tropical Australia but is widespread in the less arid parts of the temperate and subtropical regions. Even so, reports of disease have been infrequent in planted forests (table 9.1, 9.2a; Kile 1980a). Locally severe outbreaks have occurred in radiata pine in South Australia (table 9.1) and Tasmania (Kile 1980a), mountain ash in Victoria (Podger and others 1978), and slash, Honduran, and radiata pines in southern Queensland (Bolland and Brown 1981). Mortality declines in pines after about 5 years, and infection centers are small. All planted conifers (pines, Douglas-fir, and Queensland kauri) and hardwoods (eucalypts) appear susceptible to some degree (fig. 9.5), but the overall impact is minor. Kile (1980a) suggested that this may be because much of the newly planted land was converted from farming to forestry or from a natural cover of drier eucalypt forests in which *Armillaria* has a limited distribution. It is



FIGURE 9.5 — Mortality gaps in plantation of alpine ash, caused by *A. luteobubalina*. Mt. Disappointment, Victoria, Australia. (G.A. Kile)

also possible that Australian *Armillaria* species have a low pathogenicity toward many introduced tree species.

Armillaria has been more frequently reported on ornamentals and garden plants, mainly in New South Wales (table 9.2a), Victoria (Smith and Kile 1981), and Western Australia (Kile and others 1983). The disease is considered serious in Melbourne and Sydney, and losses have been recorded in the botanical gardens of Perth, Adelaide, Canberra, and Sydney (Kile unpubl., Kile and Watling 1988, Smith and Kile 1981). Attacks have also occurred in orchards and horticultural crops (table 9.2b), particularly in citrus, pome, and stone fruit orchards in most states (Doepel 1962, Kable 1974, Nicholls 1915). Other listings (table 9.2b) include attacks on bananas (New South Wales), raspberries and loganberries (Tasmania), grapes (Western Australia), hops (Tasmania), mulberry (Western Australia), passionfruit (Western Australia), and vegetables in most states (Doepel 1962, Lea 1909). The species responsible for the disease in urban gardens, fruit orchards, vineyards, horticultural crops, and ornamental trees in Australia is *A. luteobubalina* (Kile and Watling 1988, Kile and others 1983, Smith and Kile 1981). *Armillaria luteobubalina* also caused mortality in planted mountain ash in Victoria (Podger and others 1978). In southern Queensland's forest plantations, *A. novae-zelandiae* and *A. fumosa* have caused minor disease in radiata pine, and *A. pallidula* has been associated with slash and Caribbean pines (Kile and Watling 1988). Earlier records ascribed to *A. elegans* in Australia refer to *A. luteobubalina* (Kile and Watling 1988).

Armillaria occurs throughout New Zealand, and frequently kills woody hosts in parks and gardens. Reports on horticultural crops are less numerous (table 9.2b; Dingley 1969, Pennycook 1989), and according to Atkinson (1971), *Armillaria* is not important as a cause of disease in fruit orchards. *Armillaria* has infected stone and pome fruit trees in the Auckland district and on the South Island, but the impact has been comparatively minor even though individual growers have occasionally sustained heavy losses. *Armillaria* is rare in citrus fruit (Atkinson 1971), but recently, the disease has become serious in many orchards of kiwifruit on the North Island (Horner 1985, 1987, 1988, 1990a,b). Attacks originate from the stumps of felled shelterbelt trees which act as inoculum sources (fig. 9.6). The species causing disease in kiwifruit orchards is *A. novae-zelandiae* (I.J. Horner, pers. comm.).

Both *A. novae-zelandiae* and *A. limonea* are responsible for root disease in radiata pine planted throughout New Zealand where indigenous podocarp-hardwood or southern-beech forests have been cleared (fig. 9.7). Losses are spectacular in the first 5 years with up to



FIGURE 9.6 — Mortality gaps in kiwifruit orchard caused by *A. novae-zelandiae*. Te Puke, New Zealand. Gaps follow lines of stumps of willow shelterbelt trees felled 5 years earlier. (I.J. Horner)

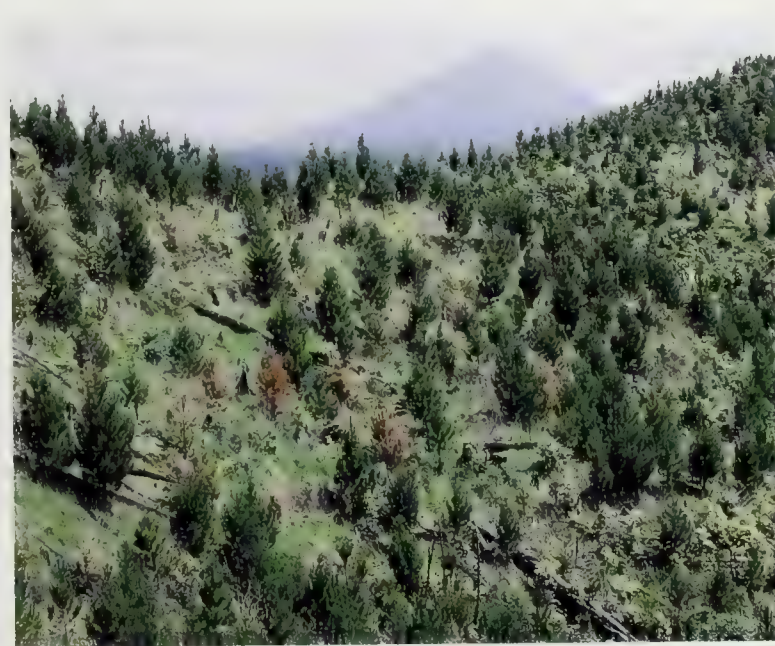


FIGURE 9.7 — Mortality gaps where young trees have been killed by *A. novae-zelandiae* and *A. limonea* in a plantation of radiata pine on a site cleared of indigenous podocarp-hardwood forest, but without stump removal (see fig. 11.1). Tuararangaia Forest, Raungaehe Range, Bay of Plenty, New Zealand. (J. Barran)

30% mortality, but may be more severe later in the rotation in the form of growth reduction and uprooting of final crop trees (MacKenzie 1987). *Armillaria* also occurs in second-rotation forests; however, its significance in these stands is unknown, but perhaps is greater than previously thought (MacKenzie and Self 1988, van der Pas 1981a).

Since the early studies of Birch (1937) and Gilmour (1954, 1966b), much has been learned about disease development in forest plantations under New Zealand conditions (Benjamin and Newhook 1984a,b; Hood and

Sandberg 1987, 1989; MacKenzie and Shaw 1977; Roth and others 1979; Shaw and Calderon 1977; Shaw and Toes 1977; Shaw and others 1976b, 1980, 1981; van der Pas 1981a,b; van der Pas and Hood 1984). This information was recently reviewed (Hood 1989), and popular accounts of the disease are available (Shaw 1976, van der Pas and others 1983).

Disease Development and Impact

Although *Armillaria* occurs in many hosts and places, the same principles govern the behavior of the disease in most plantations throughout the world. This section examines the distinctive features of plantations that influence disease development and describes the effect of infection on crop production. For this discussion, a plantation is defined as a stand or crop created by sowing seed or by planting. Coppice stands derived from adventitious shoots or suckers and forests regenerated beneath seed trees after logging are excluded. Some factors governing disease development in amenity plantings have been considered by Miller (1940), Rhoads (1956), and Rishbeth (1983).

The Significance of Plantations

Plantations differ to a greater or lesser extent from natural forest in several respects. They are often even-aged monocultures in which plants are regularly spaced at an appropriate stocking density. Various forms of selection, including clonal propagation, may give rise to planted stock with a reduced genetic base. These features are intended to facilitate crop management and ensure high product yield. However, some aspects of plantations may encourage disease.

Inoculum Potential

Attack by *Armillaria* invariably involves inoculum in the soil consisting of woody material colonized by the fungus (see chapter 4). In natural, unmanaged forests, such a food base normally becomes available sporadically as trees uproot or are killed by *Armillaria* or other agents. In plantations, by contrast, colonized stumps or debris left after harvesting a previous stand, generally by clearfelling, are particularly abundant when the crop is established and the young plants are most vulnerable.

Induced Host Stress

Root systems of naturally established seedlings growing under favorable soil conditions are normally well formed whereas those of planted seedlings are often deformed or injured. Seedlings weakened in this way are more likely to die from *Armillaria* infection than are unstressed seedlings (see chapter 7). Singh

and Richardson (1973) observed a higher incidence of mortality among bare-rooted stock than among container-grown seedlings after planting. Kessler and Möser (1974) found that plants established from seed survived *Armillaria* attack during drought stress better than planted trees (see also Buckland 1953, Thies and Russell 1984, Weissen 1981, Whitney and Timmer 1983).

Choice of Species

Planted hosts are often established outside their natural range, and may therefore be exposed to species and strains of *Armillaria* which they would not naturally encounter. Under these circumstances, introduced plants in plantations and gardens may conceivably be more prone to attack than hosts indigenous to the region although evidence to support this hypothesis is meager. Exotic spruce and firs in a Newfoundland plantation proved more susceptible to *Armillaria* than indigenous species of the same genera (Singh and Richardson 1973). In Californian walnut stands, the introduced Persian walnut is susceptible to the local species of *Armillaria*, and is therefore grafted onto rootstocks of the resistant, indigenous northern Californian walnut (Wilson and Ogawa 1979). Either exotic hosts may be inherently susceptible, or susceptibility may be induced by environmental features to which they are not adapted.

Monocultures

Deaths from *Armillaria* will be more numerous where greater numbers of susceptible plants occupy an infected site. Establishing even-aged, uniformly stocked plantations of susceptible species creates an extreme situation conducive to disease expression that may not arise in floristically and structurally diverse natural forests. Moreover, the uniform, close spacing of many monocultures may facilitate disease spread between susceptible plants. Fedorov and Poleschuk (1981) attributed greater disease impact from *Armillaria* and *H. annosum* in the Soviet Union to large-scale planting of single-species forests (cf Garrett 1956a). The general principles of disease risk in monoculture plantations have been discussed elsewhere (e.g., Gibson and Jones 1977, Peace 1957).

Disease Dynamics

Disease Establishment

Outbreaks of disease typically occur in crops or plantations that replace natural forests or earlier plantings (fig. 9.7). Inoculum consists of residual infection derived from the original forest or previous crop. This builds up on stumps and root debris (fig. 9.8; see chap-



FIGURE 9.8 — Stump of recently felled tawa tree with root system colonized by *A. limonea* on site cleared of indigenous podocarp-hardwood forest prior to burning and planting in radiata pine (see fig. 9.7). Near Rotorua, New Zealand. (I.A. Hood)

ter 4), from which it spreads to the new plants. *Armillaria* is rare in plantations established on non-forested areas such as grasslands, or arable land that has been cultivated for many decades (Gibson 1957a,b; Huntly and others 1961; Kile 1980a; Liese 1939; Rhoads 1925; Singh 1981c), although disease occasionally occurs on these sites (Fedorov and Poleschuk 1981; Gilmour 1954; Rishbeth 1978b, 1988; van der Pas 1981a). Even under these circumstances, some form of woody material such as a thinning stump is needed to establish the primary inoculum (Swift 1972). Less commonly, primary inoculum may consist of colonized wood material transported in floodwaters (Dadant 1963b, Hewitt 1936, Magnani 1978) or during land contouring prior to planting (Horner 1987). Inoculum may be introduced on wooden stakes, posts, or infected nursery stock (Kable 1974). The fungus can also invade plantations from infected trees or shrubs established for shelter or shade, or as a source of green mulching material, in both tropical (Colonial Research Pesticides Unit 1959; Dadant 1960, 1963b; Fassi 1959; Gadd 1940; Gibson and

Goodchild 1961; Leach 1936; Milimo 1989; Petch 1922, 1928; Rishbeth 1980) and temperate crops (Beaumont 1954; Chapot 1964; Horner 1987, 1988; Smith 1971).

Although the role of basidiospores has been disputed (Fox 1970, Kable 1974, Shaw 1981a, Swift 1972), current evidence indicates that the fungus may enter plantations in this form (Rishbeth 1964, 1970, 1987). Airborne basidiospores appear unable to infect living trees directly, with or without wounds (Roll-Hansen and Roll-Hansen 1981, Rykowski 1980), but they can colonize freshly cut wood during the fruiting season (Hood and Sandberg 1987, Molin and Rennerfelt 1959). Basidiospores, which may be less ephemeral than previously assumed (Shaw 1981a), may invade stumps or other debris from which infection then spreads to adjacent, living trees (Fedorov and others 1985, Garrett 1956a, Horner 1988, Petch, in Rishbeth 1955, Rishbeth 1985b).

In theory, new disease centers could be created whenever suitable woody substrates become available during a rotation. When a plantation is established, incoming spores may supplement existing inoculum derived from the previous clearfelled forest, especially if this is substantially reduced during burning of the logging debris and slash prior to planting (Hood and Sandberg 1989, Sokolov 1964). Hot fires may kill still-living stumps, rendering them more susceptible to subsequent colonization. Thinning stumps (Fedorov and others 1985; Peace 1951, 1962; Schönhar 1973) or stumps of shelter trees (Horner 1987) readily harbor the fungus and may act as sources of basidiospore-derived primary inoculum later in the rotation. In Britain, indirect but convincing evidence for basidiospore infection has been demonstrated by the occurrence of small, single-genotype clusters of *Armillaria* infection centered on thinning stumps in first rotation stands planted on former arable or heathland (Rishbeth 1978b, 1985b, 1988). In New Zealand, Horner (1988, pers comm.) has shown that infection centers in kiwifruit orchards are initiated by spores that colonize chemically killed stumps in felled willow shelterbelts (fig. 9.6).

Armillaria infects the new crop when roots of established plants encounter the primary inoculum, either through direct contact or by rhizomorphs. Infection is governed by host susceptibility, pathogenicity of the species or strain of *Armillaria*, and the frequency of root or rhizomorph contacts (see chapters 4 and 6). Rhizomorphs grow out from the inoculum source and are found mainly in the top 20 cm or so of soil (Redfern 1973; Rykowski 1981c; Singh 1978, 1981b), although in some light soils they may live in colonized stump roots more than 2 m beneath the surface (Horner 1987). They can extend laterally up to 5 m from the inoculum source (Peace 1962), but the distance over which they are able to infect host plants is probably much less (see

chapters 4 and 6). In some situations, they may serve as a bridge between roots nearly, or actually, in contact (Kable 1974).

The extent of rhizomorph development depends primarily on the species of *Armillaria* (Guillaumin and others 1984, 1989a; Rishbeth 1985b); but the soil also has an effect (see chapters 4 and 6). Rhizomorphs are rare or infrequent in certain plantations in Southeastern United States (Rishbeth 1978a, Sinclair and others 1987), low and mid-elevation parts of Africa (Anon. 1953, Bottomley 1937, Boughey and others 1964, Fassi 1959, Fox 1970, Kotzé 1935, Olembo 1972, Swift 1968, Wiehe 1952), northern India (Singh and Khan 1979), eastern China (Chang and others 1982), Papua New Guinea (J.A. Simpson, pers. comm.), Fiji (S. Singh 1978), and Australia (Pearce and Malajczuk 1990a, Podger and others 1978).

Disease Distribution Pattern

In young plantations, infected plants typically occur in groups centered on the primary inoculum (James and others 1982, Jie 1982, Peace 1962, Podger and others 1978, Swift 1972, van der Pas 1981b, Zondag and Gil-mour 1963). These groups are referred to as infection centers or disease foci. The number of dead trees in a focus is often small (Bolland and Brown 1981, Gibson 1973, Greig and Strouts 1983, Podger and others 1978, Whitney 1983). In these circumstances, the impact of mortality is probably comparatively minor since the limited land area temporarily lost to production is soon reclaimed as surviving tree root systems grow and reoccupy the site (Johnson and others 1972). However, disease centers may be larger and more significant.

The shape, size, and distribution of disease foci are governed both by the spatial occurrence of *Armillaria* in the previous stand or forest and by the distribution pattern of the residual stumps. In western North America, pathogenic *Armillaria* exists in large (often over 400 m across), centuries-old colonies (fig 8.6) in natural ponderosa pine forests (Anderson and others 1979, Shaw and Roth 1976). The same may be true in old-growth Douglas-fir stands nearer the coast (Hood and Morrison 1984). In plantations that replace these forests, many small disease centers arise, each consisting of only a few trees. All trees in every cluster over a wide area (more than 100 m across) are infected by a single *Armillaria* genotype, apparently derived from the colony of *A. ostoyae* that originally occupied the site (Adams 1974, Hood and Morrison 1984). By contrast, in selectively logged, old-growth, podocarp-hardwood rainforests in New Zealand, where *Armillaria* appears to be essentially non-parasitic, single-genotype colonies are small and densely distributed (Hood and Sandberg

1987). Disease centers in radiata pine plantations subsequently established on these sites are composed of different genotypes, some possibly originating from new introductions of basidiospore-derived material after clearfelling the natural forest (Benjamin and Newhook 1984a). In European forests, colonies of *Armillaria* species of one genotype seem to vary between about 10 m across up to 60 m (*A. ostoyae*), or to around 200 m or more for *A. gallica* and *A. borealis* (Durrieu and Chaumeton 1988; cf Rishbeth 1972a, 1982, 1985b; Siepmann 1985; Siepmann and Leibiger 1989; Thompson and Boddy 1983).

Disease distribution is also affected by the distribution of stumps in the previous crop (Roth and others 1979, van der Pas 1981b). Many small, dead trees or stumps are more likely to ensure a widespread distribution of primary inoculum than are a few large ones (Pronos and Patton 1977), except when stumps are too small to act as effective inoculum.

Secondary Disease Spread

The primary inoculum eventually declines as a source of infection although the time required varies with stump size and host species. On some sites, hardwood stumps may act as inoculum for up to 30 years whereas conifers decompose more rapidly (Ivory 1987, Wingfield 1987). Whether the disease continues to spread through the plantation beyond the original infection center depends on whether or not infection is transmitted between healthy plants and adjacent infected plants of the same crop (the secondary inoculum). Secondary disease spread occurs in the same manner as primary spread (by root or rhizomorph contacts) and also by root grafting (Buckland 1953, Greig and Strouts 1983, Hintikka 1974, Peace 1962). It is limited by the distance between roots of neighboring trees and probably by the inoculum potential attained on infected hosts. Infected herbaceous plants, such as those found in vegetable or flower crops, are themselves unlikely to achieve sufficient inoculum potential for secondary disease spread; it is probable that only the initial, primary inoculum is functional in such plantings (Peace 1962, cf Wilson 1921, 1932). Rishbeth (1972b) suggested that very young, infected pine seedlings may also be too small to act as effective secondary inoculum, although apparent secondary spread has been observed among densely packed seedlings of radiata pine sown in nursery beds (pers. obs).

Van der Pas (1981b), working with radiata pine up to 5 years old in New Zealand, monitored mortality rates that followed van der Plank's (1963) model for disease increase without multiplication (slope of $\log_e [1/1-x]$ linear with time; x = proportion of dead trees) and

concluded no secondary spread happens in very young plantations (*cf* Whitney 1988b). On the other hand, Swift (1972) fitted mortality rates in up to 8-year-old slash pine in Zimbabwe to the model for disease increase by multiplication (slope of $\log_e [x/1-x]$ linear with time), implying that tree-to-tree spread of infection had occurred. Examining these results suggests that data from both authors may be used in either model with an acceptable degree of probability; conclusions based on this statistical method should be treated cautiously.

Other factors that govern the rate of spread of both secondary and primary disease are discussed in chapters 5, 8, 10 and 11. In addition, spread of disease may depend on the presence of susceptible carrier weed species (S. Singh 1978). Horner (1987) found that infection moved along kiwifruit roots faster than rhizomorphs grew through the soil. At times, these factors effect different rates of spread in different directions and thus distort shapes of disease foci. For example, infection frequently spreads along planting rows (fig. 9.6) giving rise to elongated disease centers (Horner 1985, Marsh 1952, Rishbeth 1978b, S. Singh 1978). Kable (1974) observed a directional trend toward irrigation channels in a peach orchard. Average rates of extension of disease centers are about 1 to 2 m per year (Chipompha 1987, Ivory 1987, Kable 1974, Pearce 1984, Podger and others 1978, Rishbeth 1980, Shaw and Roth 1976).

Subsequent Disease Development

Little is known about how infection centers behave in older forest plantations, but their boundaries might be expected to become more diffuse and irregular, and centers may merge and coalesce (McNamee and others 1989, P. Singh 1981c, Stage and others 1990). If *Armillaria* is widely distributed, the disease may affect randomly scattered trees rather than form discrete centers. MacKenzie (1987, *cf* Bloomberg and Morrison 1989) hypothesized a state of disease equilibrium in an older radiata pine plantation. He observed that although the percentage of basally infected trees remained fairly constant at 50-60% between ages 10 and 19 years, the root collars on 31% of the trees recovered from infection over this period while those on a slightly higher percentage of trees became newly infected. Chronically infected trees, often without crown symptoms (see chapter 5), have been reported in several forest plantations (Plavšić 1979, Rykowski 1980, Singh 1981c, Whitney and others 1989a); planted trees can resist and often recover from infection (Boullard and Gaudray 1975, Courtois 1979, Johnson and others 1972, Kawada and others 1962, Plavšić 1979). Observations in certain natural stands suggest that faster-growing trees may be more prone to chronic infection because their larger root systems are more likely to encounter the inoculum (Bloomberg and Morrison 1989, Hřib and others 1983).

Very little information describes how disease develops in successive crops planted on the same site except that *Armillaria* persists in subsequent rotations in both forest plantations and orchards (New Zealand For. Res. Inst. 1954; Delevoy 1946; Gibson 1957a,b, 1960, 1967; Holmsgaard and others 1961; Huntly and others 1961; Lundquist and Baxter 1985; Lysaght 1944; Millard 1949; Salmon and Ware 1937; Sisson and others 1978; Swift 1970; van der Pas 1981a). Knowledge is sparse partly because forest plantations which represent second or subsequent rotations are still uncommon and because in non-forest plantations the rotation status of the crop or stand is often unknown. Some authors considered that inoculum may dwindle and disappear after several rotations of conifer species (Gibson 1975, 1979; Peace 1962; S. Singh 1978; Wingfield 1987), but Redfern (1975) reported examples of disease in second- and third-rotation conifer crops following indigenous hardwoods. Inoculum may possibly increase in successive forest plantations, and Garrett (1956a) warned of a potentially greater need for eradication measures in planted stands than in natural forests. Multiple cropping may even introduce inoculum where it did not formerly exist (Delevoy 1946, Rishbeth 1978b). *Armillaria* currently inhabits certain second-rotation radiata pine stands in Kaingaroa Forest, New Zealand, on sites not formerly covered in indigenous forest (Gilmour 1954, MacKenzie and Self 1988, van der Pas 1981a). Planting young stock among established trees is another practice likely to enhance inoculum in diseased orchards (Kable 1974). This procedure, like multiple cropping, may also select for particular *Armillaria* species.

Stress and Predisposition

Disease development in plantations is influenced by two seemingly contradictory hypotheses of pathogen-host interaction often encountered in the literature. Some workers believe that *Armillaria* attacks secondarily or opportunistically (see chapter 7), being serious only on trees predisposed by various physical or biotic agents (Buckland 1953, Gremmen 1976, Huntly and others 1961, Johnson 1976, Sinclair and others 1987). Alternatively, attack may be primary; numerous examples in the literature confirm that vigorous plants may be directly infected (see chapter 6).

Whichever situation applies in a plantation probably depends on circumstances. *Armillaria* may be directly pathogenic on susceptible plant species but an opportunist on weakened, normally resistant hosts. Even so, it is not an easy matter to determine what is really occurring, due to the difficulty of deciding whether or not a host plant is actually under stress (Hiratsuka 1987, P. Singh 1980b). A major consideration is the pathogenicity of the *Armillaria* species concerned (see chapter 6; Guillaumin

and others 1984, 1989a; Rishbeth 1982, 1985b) and its inoculum potential (see chapter 4). Peace (1962) suggested that a three-way balance exists between the pathogen, the infected host, and the environment (*cf* Davidson and Rishbeth 1988, Sinclair and others 1987). Physiological host stress disturbs this balance in favor of the pathogen (Gibson and Goodchild 1961). The effect of stress on the host-pathogen interaction in both natural stands and plantations is discussed in chapter 7.

Disease Loss

Loss and Crop Age

In perennial plantations, the type and extent of disease loss is often closely related to the age of the crop (Rishbeth 1972a). In forest plantations, particularly those of conifers, mortality is the most common expression of disease early in the rotation since younger trees tend to be more susceptible and less tolerant of infection (Gibson 1975, Ivory 1987, Peace 1962, Sinclair and others 1987). In some stands, most mortality occurs during the first 8 years or so after planting (Bolland and Brown 1981, Fedorov and Poleschuk 1981, Fuller and James 1986, Longenecker and others 1975, Pronos and Patton 1977, Redfern 1978, Shaw and Calderon 1977, Ušćuplić 1980, van der Pas 1981a), while in others mortality may continue for at least 25 years (Johnson and others 1972, Morrison 1981, Pearce 1984, Singh and Khan 1979, P. Singh 1981c). Comparatively early peak attack is also recorded in crop plants such as cinchona (Chevaugneon and Merny 1956), rubber (Anon. 1950, Pichel 1956), mulberry (G.-C. 1927), oil palm (Anon. 1948-1950, 1958), olive (Leach 1931), and tea (Gadd 1928-1930). However, in some plantation species, such as fruit trees (Hendrickson 1925, Kable 1974) and chestnuts (Bazzigher 1956), killing is less closely related to age. Marsh (1952) found older apple trees to be more susceptible in Great Britain.

Armillaria can kill even large specimens of some species; and significant losses may occur in older forest plantations or in urban plantings, particularly if trees are stressed (Greig and Strouts 1983; Kawada and others 1962; Mańka 1953, 1980, 1981; Moriondo 1981; Podger and others 1978). However, production losses in older stands are more often caused by growth reduction, butt rot, breakage, and windthrow, as a result of chronic infection (Dariichuk 1986 a,b).

Growth reduction due to *Armillaria* infection is rarely reported in annual crops (Connors 1936) and only occasionally in perennial horticultural plantations, possibly because reduced fruit yield is a more meaningful parameter of production loss (e.g., grape vines: Nieder 1980, Sisson and others 1978; kiwifruit: Horner 1985). Reports of growth reduction are more frequent from forest plantations (Peace 1962, Sinclair and others 1987,

Williams and others 1989, *cf* Hřib and others 1983), but even in these crops, values are often presented only for tree height or stem diameter. Wood volume loss is rarely quantified (Morrison and others 1988, Shaw and Toes 1977, P. Singh 1980b, Terashita and others 1983). In older forest plantations, the increment of chronically infected trees can be depressed for extended periods although fluctuations may occur if circumstances change (Shaw and Toes 1977). By contrast, in acutely infected trees, which are usually relatively young, growth may drop sharply for 1-2 years prior to death (Lundquist 1988, Morrison 1981, Podger and others 1978, Szukiel 1980).

As trees of certain species become older, infection progresses from the roots to the lower stem heartwood. Butt rot caused by *Armillaria* is frequently present in older forest plantations, often associated with other decay fungi (Kató 1967b, Schönhart 1969, Storozhenko 1974, Yde-Andersen 1958, Zhukov 1968). Decay is also occasionally reported in other perennial crops such as fruit trees (Adaskaveg and Ogawa 1990, Guillaumin and others 1989b, Petersen 1960). The extent of rot depends on the host species (Greig and Strouts 1983, Peace 1962) and also on the species of *Armillaria*. In Britain, conifers are decayed mainly by *A. ostoyae*, *A. borealis*, and *A. cepistipes* whereas hardwoods are decayed by *A. gallica* (Gregory 1989, Gregory and Watling 1985, Rishbeth 1982).

Decay seldom extends more than a meter or so above ground level, depending on tree size, but it may be slightly more extensive in hardwoods than conifers (Greig and Strouts 1983). Even so, wood destruction represents volume loss from the more valuable butt log section, and the impact of this damage may therefore still be significant (Pegler and Gibson 1972). Losses also occur in butt rotted trees through stem breakage and windthrow (Greig and Strouts 1983, Ivory 1987, Moriondo 1981, Murray 1959, Sinclair and others 1987, Singh 1981c). The impact of windthrow and growth loss later in the rotation is probably more serious than that of early mortality since residual trees no longer balance the loss by compensatory growth during the remainder of the rotation (MacKenzie 1987). Butt rot also occurs in natural forests, and is discussed further in chapter 8 (which also includes examples from plantations, reference table 8.2).

Evaluation of Disease Impact

The overall economic loss caused by *Armillaria* root disease in plantations is rarely quantified effectively, probably due to the difficulties involved and the effort required. If attack is secondary, it is almost impossible to distinguish loss due to the predisposition stress from that caused by subsequent *Armillaria* infection (Chabro-

lin 1924, Hiratsuka 1987, Singh 1980b). For a complete and comprehensive economic evaluation, all aspects of disease loss, including uprooting, breakage, and less obvious effects of chronic infection such as growth loss and butt rot, must be considered.

Most disease impact assessments in forest plantations contain either qualitative comments such as “of no importance,” “severe attack,” “scattered mortality,” or numerical estimates of the proportion of trees killed. Mortality is the most dramatic expression of the disease, and estimates have ranged from less than 3% (Morrison 1981, Singh and Khan 1979) to more than 50% (Ivory 1987, van der Pas 1981a). Mortality loss may be underestimated if counts are not made at regular intervals since small dead trees soon become lost among surrounding weed growth. On the other hand, Gibson (1979) suggested that the impact of mortality may be over-emphasized, at the expense of that due to chronic infection, because of its often spectacular appearance. Lower levels of mortality can represent a form of natural thinning, and are significantly compensated by increased growth of remaining trees (Courtois 1979, MacKenzie 1987). Other methods of impact assessment (see chapter 5) have been used, all of which to some extent underestimate the total economic loss. These methods include percentage of plantations or stands diseased in a forest, area or proportion of forest area out of production as a result of the formation of mortality gaps (Filip 1979, Jie 1982, Podger and others 1978, Redfern 1978, Shaw and Calderon 1977), and height (Singh 1981c) or diameter (Shaw and Toes 1977) increment reduction (see Lundquist 1988).

Occasional attempts have been made to assess the total loss throughout a rotation. Gibson (*in* Oforu-Asiedu 1980) presented estimates of annual wood volume losses from conifer plantations in Malawi. Johnson and others (1972) judged that mortality gaps in plantations on Vancouver Island in British Columbia, Canada, were not of sufficient area to support a 48-year-old tree. They concluded the disease would have little impact by age 40-50 years as long as gaps did not expand and assuming that infected trees with healing stem lesions would recover. Shaw and Calderon (1977), and later MacKenzie (1987), evaluated the losses in a radiata pine stand in New Zealand. It was estimated that *Armillaria* reduced volume production by 6-13% in stands with a projected rotation length of 28 years (MacKenzie 1987).

Mortality more appropriately measures loss in orchards and horticultural crops than in forest plantations. Some reports containing estimates of disease impact in orchards or other non-forest crops are given in Division of Botany, Department of Agriculture (1923) and by Leefmans (1927), Zeller (1932), Pastore

(1955), and Horner (1987). In contrast to forest plantations, it is normally economically feasible to replace diseased trees in orchards.

The impact of *Armillaria* in ornamental hosts varies greatly (Rhoads 1956). Losses are often high but difficult to express in economic terms because of the problem of assigning monetary values to plants grown for their aesthetic appeal. Costs can be quantified, however. These include control measures, removal of dead plants, stumps, and roots, site preparation or restoration, and the purchase of replacement plants. Although the expenses incurred by individual landowners are usually relatively low, the aggregate costs of *Armillaria* root disease in amenity plantings may be substantial.

Plantation Management and Disease

Control of *Armillaria* by reducing inoculum and other means is discussed in chapter 11. This section considers how routine tending procedures carried out in forest and horticultural plantations may indirectly influence disease severity, often without reducing the amount of inoculum. In practice, cultural management is rarely conducted specifically for disease control because such operations are costly and because reliable information on the expected economic gains is lacking (*cf* Pawsey and Rahman 1976a).

Planting

Young plants must always be considered vulnerable when exposed to a high inoculum potential. Using healthy, vigorous stock (Magnani 1978) and observing good planting practice (Birch 1937, Buckland 1953, Hadfield and others 1986, Johnson 1976, Ono 1970, Thies and Russell 1984) can minimize stress for trees planted on infected sites. The need for care at time of planting is supported by field observations (see also examples under “induced host stress”). Klomp and Hong (1985) found significantly higher *Armillaria* mortality among rooted radiata pine cuttings than among planted seedlings. They attributed this to better developed root systems on the latter. Hall and others (1971) observed the disease in planted seedlings whereas natural regeneration was unaffected. A number of authors have recommended using seed or container stock rather than bare-rooted plants in order to reduce plant stress (Hiratsuka 1987, Kessler and Möser 1974, Singh and Richardson 1973, Weissen 1981), but Shaw and Roth (1978) noted that other management considerations do not always permit this.

In theory, dense planting might be expected to favor disease spread due to competition stress and earlier root contact with adjacent plants. However, very little

field or experimental evidence documents the influence of planting density on disease (Hiley 1923). Pielou and Foster (1962) did not find a relationship between density and disease severity in Douglas-fir plantations, and attributed this to the fact that all the stands they examined were already old enough for root contact to have occurred.

Cultivation and Weed Control

Cultivation between rows of plants is a routine procedure in many orchards or planted crops. This practice controls weeds and improves soil texture, but it may also influence development of *Armillaria* root disease (Cutuli and Privitera 1986). Injuries sustained by crop plants during cultivation can cause stress and reduce disease resistance (Rosnev and Tsanova 1976). On the other hand, movement of infection across cultivated ground may be interrupted by the severing of roots. In a black currant plantation, Marsh (1952) observed a greater spread of disease along rows separated by parallel strips of cultivated ground than between rows. However, cultivation may also stimulate fresh growth from the cut ends of damaged rhizomorphs (Redfern 1973, Rykowski 1981c, Sewell 1965).

The amount of weed growth in a plantation is another factor that may influence disease development. Weeds may stress crop plants in young plantations through competition, especially in areas subject to droughts, rendering them more susceptible to infection, or damage if already infected. In addition, weeds may serve as bridges to promote disease spread between plants (Shaw and others 1976b, Singh and Bola 1981). However, using herbicides to kill weed growth or unwanted shade or shelterbelt trees may also increase disease severity by providing additional inoculum substrate (Andruszewska 1973, Boyd 1986, Pronos and Patton 1977, Schütt and others 1978). Cutting woody weed species may similarly enhance inoculum if root systems die and become colonized by the fungus. Application of certain herbicides may promote or inhibit the growth of *Armillaria* itself (Andruszewska 1973).

Thinning and Pruning

Little information describes how thinning impacts disease in forest plantations. Filip (1989a) found that thinning a number of conifer plantations had no significant effect on *Armillaria* mortality 5 years later.

Two factors in particular influence disease development when stands are thinned. Thinning may promote resistance to disease by reducing competition among residual trees (Johnson 1976, Singh 1981c, Williams and others 1989). Davidson and Rishbeth (1988) found that

A. mellea, *A. ostoyae*, and *A. gallica* all caused extensive infections in oaks and pines weakened by crown suppression whereas only limited infections by *A. mellea* and *A. ostoyae* occurred in unsuppressed, subdominant oak and pine trees, respectively. On the other hand, thinning increases the amount of inoculum in a stand by providing fresh substrates for colonization, as noted earlier (refer under "disease establishment").

Thinning may affect diseased stands in other ways. It may lead indirectly to an unacceptably low stocking density if infected trees continue to die after the final thinning (Morrison 1981). Disease may be encouraged in final crop trees through stress from logging damage during commercial thinning (Johnson 1976).

The timing of thinning operations might be expected to influence the level of disease in plantations, but no information is available about the precise effect. Rishbeth (1978b) suggested that thinning late in the rotation may result in fewer, smaller, new disease centers, and so result in carryover of less inoculum into the subsequent rotation. Alternately, the bigger stumps created by late thinning may enable the fungus to develop a greater inoculum potential than on the smaller stumps from earlier thinnings. This could result in larger foci.

The stress of pruning live branches is likely to be harmful to plants already infected by *Armillaria*. However, the effects of pruning on the disease are even less studied than thinning. Chronically infected radiata pine trees were observed to die shortly after being pruned in a New Zealand stand (C.W. Barr, A. Zandvoort, pers. comm.). Excessive pruning of infected trees has also had serious effects in fruit orchards (Stahel 1950).

Fertilization

In many plantations, especially orchards and horticultural cultivations, application of fertilizers is an often routine part of management. Such treatment may especially benefit chronically infected plants stressed by nutrient deficiencies. However, other effects may also occur. Greater root growth may increase the chance of encounter with inoculum. Development of the inoculum itself may be promoted or discouraged by particular soil amendments (see chapter 4).

Fertilizer treatments have generally benefited diseased plants in several field trials, but definite results are not always observed, suggesting that complex interactions are involved. Singh (1983) showed that trees potted in a nutrient-rich soil (pH 4.8) were larger, became infected later, and had a smaller proportion of roots infected than plants in a soil deficient in certain nutrients (pH 3.8). Infection and mortality were lower in the fertile

soil and plants demonstrated active resistance by resin bleeding and callus formation. In a series of field trials in young pine plantations, Rykowski (1976b, 1980, 1981a, 1983) in many cases also demonstrated improved health to chronically infected trees after fertilizers were applied, although mortality rates were largely unaffected. Fertilizing appears to correct partially the tendency for root collar infection to hinder uptake of nitrogen and magnesium (Rykowski 1981b). Spurling and Spurling (1975) found that the damage caused by *Armillaria* in cultivated banana plants was reduced by applying potassium fertilizers. Clearly, additional trials are required before the effects of fertilization can be exploited in specific cases. Further work is also needed to clarify the effect of lime application on disease development (Anon. 1950, Pawsey and Rahman 1976a, Shields and Hobbs 1979, Sokolov 1971, van der Pas and Hood 1984).

Fertilizing with organic material is not always beneficial. Soil applications of processed urban refuse increased the incidence of disease in plantations established on infected sites, due apparently to host stress caused by toxic matter in the waste materials (Courtois 1973, Schwarz and Zundel 1975). Even so, Courtois (1979) found that trees which survived on sites treated in this way were larger than untreated plants. This was attributed either to the direct effect of the organic additive or to the "thinning" response among residual, surviving trees.

Control of Other Pests or Diseases

Trees with chronic *Armillaria* infection may succumb to other debilitating pest or disease agents present in plantations (see chapter 7). Relieving stress by routinely controlling these disease organisms or agents may promote resistance to *Armillaria*. Copper-based fungicide sprayed to control *Dothistroma* needle blight [*Dothistroma septospora* (Dorong.) Morelet (*D. pini* Hulbary)] in radiata pine stands in New Zealand reduced the impact of *Armillaria* in a chronically infected stand (Etheridge 1968, Shaw and Toes 1977).

Conclusions

Reports in the literature during the past 60 years indicate that species of *Armillaria* cause root disease in many planted hosts throughout the world. Attacks occur in softwood and hardwood forest plantations, woodlots, hedgerows, shelterbelts, orchards, and horticultural crops. The disease is also widespread in shade and amenity trees, ornamental shrubs, and herbaceous plants established in gardens, parks, and on roadsides. Records are particularly numerous from Europe, North America, Africa, and Australasia, but the disease is also present in the Soviet Union, Asia, and South America.

In tropical parts of East Africa, Southeast Asia, and South America, it occurs in plantations at higher elevations where the climate is comparatively cool and moist.

Attack typically occurs in plants established on sites formerly occupied by forests or orchards, and in hosts interplanted among infected trees in existing stands. Infection spreads to new plants when roots encounter rhizomorphs growing from stump roots or when crop roots directly contact roots of colonized stumps. Plants tend to become infected in groups centered on stumps or root inoculum present in the soil, and deaths give rise to unstocked gaps. As the primary inoculum decays and becomes ineffective, disease centers may expand in perennial plantations through the creation of secondary inoculum in the crop itself. The rate of secondary spread between adjacent plants is governed mainly by host susceptibility, the degree of interaction between neighboring root systems, and the effectiveness of root-to-root transmission of infection. The subsequent development of disease centers in older plantations is not well understood.

Despite the merits of planting, and the obvious necessity of growing food crops and forest trees in plantations, several features of these production systems tend to encourage disease development when *Armillaria* is present. On previously wooded sites, inoculum increases to a high level early in the rotation when plants are young and especially vulnerable; new plants are predisposed to disease through transplant stress and the malformation of root systems; and spread of disease is favored by close spacing of even-aged stock. In monocultures the whole crop may be composed of a species susceptible to infection.

Mortality is the most obvious form of disease loss in young perennial plantations, while growth reduction, butt rot, lower stem breakage, and uprooting characterize chronic infection in older planted stands. Although often less spectacular than early mortality, chronic disease may have a more significant economic impact in forest plantations, but production loss has rarely been reliably quantified. The incidence of mortality is commonly quoted but has limited value unless disease centers are large, because increased growth of residual trees tends to compensate for earlier losses in tree numbers. The financial losses in ornamentals are difficult to quantify, and the cost of remedial measures may be underestimated in such plantings.

Disease development in infected plantations can be influenced by various management practices, such as the application of fertilizers, but choice of species, planting density, and the timing and intensity of thinning probably have the greatest effect in forest crops

(see chapter 11). Apart from using less susceptible species on infected sites, operations are rarely conducted specifically to ameliorate the impact of disease due to uncertainty about the effectiveness of such procedures

and about their economic benefit. Further research is required to identify management regimes which will maximize returns from infected plantations.

TABLE 9.1 — *Armillaria* in planted conifer hosts, by country^{1,2}

World zone	Continent	Country (and region)	References ²
North Temperate	America (North)	Canada (General)	65. 2260
		Canada (BC)	41. 98; 42. 544; 57. 70; 63. 160; 73. 4051 (FA); 82. 7166 (FA); 85. 787; 86. 1121
		Canada (Ontario)	56. 799; 62. 418; 72. 1946; 73. 2753; 80. 941; 84. 374 (FA)
		Canada (Queb. & Maritime Provs.)	58. 380 (?), 684 (?); 62. 418; 63. 223; 67. 158b; 68. 1315; 71. 3387o; 86.312 (FA)
		Canada (Newf.)	63. 223; 70. 257a, 3032; 71. 3213; 74. 1670 (FA); 75. 958 (FA), 980 (AE); 79. 3084 (FA); 80. 5607 (FA); 82. 1632 (FA), 1969, 3079, 4411 (FA); 83. 10258 (SF); 84. 914
		USA (General)	86. 4102
		USA (Calif.)	48, 545 (ornamental?); 54. 79 (ornamental)
		USA (Wash., Ore., Idaho)	74. 6995 (FA), 7692 (FA); 76.420; 77. 4229; 80. 2375; 84. 2840 (FA)
		USA (New Mexico)	72. 1995
		USA (Minn., Wis.,Ind.)	28. 685; 60. 355; 77. 3733
			(WA); 79. 3474; 83. 4468 (FA); 84. 5574 (FA)
		USA (Penn., NY, Conn.)	26. 394 (ornamental); 62. 259; 76.3873 (FA)
		USA (Georg., Fla.)	44. 504 (ornamental); 45. 435 (ornamental); 71. 1461; 73. 2051
	Asia	India (North)	56. 405; 80. 3431; 83. 4248 (FA)
		Japan	62. 551; 63. 499; 66. 635; 71. 2001
	Atlantic	Portugal (Azores)	62. 487; 72. 4380; 77. 5835
	Europe (Western)	Belgium	29. 147; 36. 473; 46. 482; 49. 51; 50. 187; 82. 1971 (FA)
		Denmark	27. 447; 28. 351; 59. 633; 61. 497, 635; 62. 69
		Eire	40. 177; 45. 38
		Finland	40. 54; 47. 222 (ornamental?); 73. 1706; 75. 2738 (FA)
		France	23. 431; 27. 586; 33. 798; 67. 2120; 68. 90; 73. 880, 1290; 74. 6724 (FA); 77. 292 (FA); 82. 364 (FA), 1915 (FA), 4359; 86. 2211, 2438, 2441
		German Fed. Rep.	28. 349, 351; 31. 354, 698; 33. 739 (?); 38. 85; 40. 177; 52. 534; 55. 6, 760; 56. 800; 66. 2266; 68. 2882b; 70. 585, 2681; 73. 6898 (FA); 74. 220 (FA), 3031 (FA), 4396 (FA); 78. 3494 (FA); 82. 1368 (FA); 84. 875; 85. 3996
		Italy	50. 185, 188; 53. 460
		Netherlands	40. 195; 58. 745
		Norway	51. 202; 66. 2978; 80. 4799
		Sweden	38. 752 (ornamental)
		Switzerland	28. 351; 33. 195; 54. 570; 55. 328; 57. 69; 58. 560
		United Kingdom	27. 197, 447; 29. 78; 33. 130; 35. 803; 38. 715; 40. 405, 506; 46. 428; 51. 591; 57. 601 (orna mental); 59. 714; 62. 262; 63. 349; 64. 1164, 3023; 66. 888; 67. 3213; 68. 2564; 71. 2000; 72. 4375d; 73. 3431; 75. 2125 (FA); 76. 6820 (FA); 78. 4869 (FA); 79. 3491; 80. 5923; 82. 5974; 85. 2171; 86. 381, 2440; 88. 3140

TABLE 9.1 — (Continued)

World zone	Continent	Country (and region)	References ²
South Temperate	Europe (Eastern)	Czechoslovakia	27. 213; 28. 351; 45. 257; 76. 2984 (FA); 79. 856 (FA); 83. 1921 (FA); 84. 935; 87. 5207 (FA)
		German Dem. Rep.	28. 351; 31. 699; 32. 141; 33. 480, 739 (?); 37. 647; 75. 4853 (FA)
		Poland	26. 714; 45. 257; 53. 44; 54. 391; 55. 499; 62. 552; 64. 2416, 2433; 69. 936; 73. 3875 (FA); 74. 3001 (FA), 5258 (FA), 7504 (FA); 75. 1556 (FA), 7809 (FA); 78. 2234 (AE); 81. 730 (FA), 3032 (FA), 4126 (FA); 82. 381 (FA), 419, 2273 (FA), 3631 (FA); 84. 919; 85. 3770 (FA), 4827 (FA), 6070 (FA); 86. 5200; 87. 1573 (FA), 1893 (FA)
	USSR	Rumania	72. 3608
		Yugoslavia	76. 4309 (FA), 4312; 81. 6678; 82. 1632 (FA)
		Soviet Union	28. 415; 65. 1283; 66. 1528; 75. 6374
		(western, incl. Belorussia, Ukraine, Caucasus)	(FA); 81. 4516 (FA), 6092; 86. 3004; 87. 2082, 2411 (FA), 4716 (FA)
	Africa	Soviet Union (Urals, Krasnoyarsk)	62. 417; 65. 1281 (?), 1978 (?)
		South Africa	33. 142; 34. 425; 37. 355, 784; 54. 657; 56. 405; 81. 2785; 83. 2174; 88. 1500
	America (South)	Brazil (southern)	64. 2095; 67. 2848
		Chile	63. 350; 65. 552; 67. 3227
	Australasia	Australia	23. 298; 71. 3384f; 82. 1632 (FA)
		New Zealand	34. 533; 38. 714; 45. 297; 53. 52; 54. 328, 329; 55. 267; 56. 565; 63. 156, 635; 69. 618c; 74. 2453 (FA); 82. 2277 (FA); 85. 2889 (FA)
Tropics	Africa	General	82. 1634 (FA)
		Kenya	51. 141, 309; 54. 16; 58. 116, 190; 60. 509=61. 569; 61. 436; 65. 2615a
		Malawi	49. 200; 53. 669
		Mauritius	46. 52
		Tanzania	52. 225; 55. 350; 65. 1924, 2615a
		Zimbabwe	62. 762; 63. 727; 68. 3020; 72. 4431
	America (Central) /Caribbean	Jamaica	68. 2958a
	America (South)	Peru	78. 3635
	Oceania	Fiji	65. 1351b
		USA (Hawaii)	65. 849 (FA); 74. 6994 (FA)

¹Published reports of *Armillaria* attack in coniferous plantation forests (with occasional records for ornamental plantings). All listings (except two) refer to Northern Hemisphere host genera, including tropical pines: *Abies*, *Cedrus*, *Chamaecyparis*, *Cryptomeria*, *Cupressus*, *Juniperus*, *Larix*, *Metasequoia*, *Picea*, *Pinus*, *Pseudotsuga*, *Thuja*, *Tsuga* (exceptions: 51.141 for Kenya and 53. 669 for Malawi, concerning *Araucaria*, *Callitris*, *Widdringtonia*). References to trees attacked within their natural distribution ranges (mainly North Temperate) are sometimes doubtfully included; it is not always clear whether these are planted or naturally seeded.

²Sources: Review of Plant Pathology (Review of Applied Mycology), unless otherwise stated.
Code: year (**not** volume No.). No. of abstract or [prior to 1964] page (abstract journal title abbreviation, as applicable).
AE, Review of Applied Entomology, Ser. A; FA, Forestry Abstracts; hA, Helminthological Abstracts, Ser. B; HA, Horticultural Abstracts; PB, Plant Breeding Abstracts; SF, Soils and Fertilizers; WA, Weed Abstracts.
Compilation: 1922-1972, manual search (keywords: ARMILLARIA, CLITOCYBE TABESCENS)
1972-June 1988, computer search (descriptor: ARMILLARIA () MELLEA; Commonwealth Agricultural Bureaux Dialog Information Retrieval Service; duplicate reports not listed).

Table 9.2a — *Armillaria* in planted, non-conifer (angiosperm) hosts, by country.(a) Species used in commercial forestry, for shelter, or as ornamentals^{1,2}

Host group	World zone	Continent	Country (and region)	References ²
Northern deciduous broadleaf trees (e.g., beech, <i>Fagus</i> birch, <i>Betula</i> ; chestnut, <i>Castanea</i> ; elm, <i>Ulmus</i> ; oak, <i>Quercus</i> ; poplar, <i>Populus</i> ; willow, <i>Salix</i>)	North Temperate	America (North)	Canada (Ont.)	64. 1755 (?)
			Canada (Queb., Newf.)	62. 418(?); 74. 1669 (?;FA); 83. 4775
			USA (Calif.)	59. 178; 71. 3187
			USA (Central & East)	32. 411; 41. 183; 42. 272; 76. 7439 (AE); 87. 78
			USA (Mississ., Fla.)	44. 417; 51. 1332 (?;FA);70. 864
		Asia	Chinese Peoples' Rep.	47. 421
			Japan	60. 354
			Pakistan	88. 5414 (FA)
		Europe (Western)	Belgium	73. 6416 (FA)
			France	23. 431; 24. 5, 8; 27. 586; 28. 290; 45. 436; 47. 320; 66. 626; 82. 364 (FA); 84. 3385 (FA), 6619 (FA); 85. 5785 (FA); 86. 2211, 2438 , 2441
			German Fed. Rep.	70. 1156; 72. 3694k
			Italy	54. 568; 61. 493; 64. 3033; 79. 1785 (FA); 81.4684
			Netherlands	31. 696; 40. 195
			Spain	64. 846
			Switzerland	57. 69 (?), 673; 61. 492
			United Kingdom	24. 244; 27. 198; 28. 126; 46. 428; 48. 399; 70. 1157; 72. 2871b; 74. 7708 (FA); 79. 899; 82. 1632 (FA), 5974; 83. 4450; 85. 2171; 86. 381, 2440
		Europe (Eastern)	Bulgaria	81. 3154 (FA)
			Hungary	86. 781
			Poland	74. 1768 (FA); 81. 3032 (FA); 87. 2326 (FA)
			Yugoslavia	26. 705 (?); 27. 5 (?); 30. 278
Other hardwood trees (e.g., <i>Acacia</i> ; <i>Casuarina</i> ; <i>Eucalyptus</i> ; <i>Grevillea</i> ; <i>Leucaena</i> ; teak, <i>Tectona</i> ; <i>Terminalia</i>)	South Temperate North Temperate	USSR	Soviet Union (western, Novosibirsk)	59. 426 (?); 66. 1528 (?); 69. 2009
		Africa	South Africa	27. 237
			Australasia	55. 285
		Africa	Tunisia	71. 285, 1396
			America (North)	28. 494; 71. 3187 (?); 80. 500 (FA)
		America (North)	USA (Calif.)	30. 159; 41. 563; 42. 486, 497; 44. 417, 504; 48. 279; 51. 1332 (FA); 53. 406; 57. 560
			USA (Fla.)	70. 1156 (?)
			Europe (Western)	86. 781
			Europe (Eastern)	33. 142; 37. 784; 88. 1500
		Africa	South Africa	59. 564 (?);77. 3 (hA; ?);82. 1632 (FA)
			Australasia	27. 19
		Tropics	Ghana	51. 141; 60. 214, 509; 61. 569; 82. 7157 (FA)
			Kenya	55. 107, 451
			Madagascar	29. 202; 40. 311; 53. 669
			Malawi	30. 507; 52. 537; 60. 633
			Mauritius	

Table 9.2a — (Continued)

Host group	World zone	Continent	Country (and region)	References ²
Shrubs and ornamental herbs	North Temperate	America (South)	Tanzania	33. 201; 36. 746 (?); 52. 225; 67. 1348
			Uganda	24. 509; 27. 15
			Zaire	51. 512
			Zimbabwe	62. 126, 761; 63. 727
			Peru	78. 3635
		Asia	India (south)	60. 123; 64. 558
			Indonesia (Sumatra, Java, Sulawesi)	25. 79; 31. 525
			Sri Lanka	28. 745; 29. 470; 31. 275
		America (North)	USA (General)	33. 696
			USA (Wash., Ore.)	32. 786; 48. 134; 70. 1677
			USA (Calif.)	54. 79; 59. 147; 68. 2734; 69. 874; 72. 1551; 80. 1616
		Europe (Western)	USA (Fla.)	42. 497; 44. 504; 48. 23; 51. 1332 (FA); 57. 560
			France	72. 4086; 82. 4011; 86. 2211, 2438
			German Fed. Rep.	70. 1156
			Italy	86. 4983
			Netherlands	40. 195
			Switzerland	57. 69
			United Kingdom (incl. Jersey)	29. 628; 32. 376; 35. 366; 36. 478; 38. 823; 48. 462; 53. 332; 54. 484, 605; 61. 267; 64. 2792; 85. 2211; 86. 381
		Europe (Eastern)	Czechoslovakia	70. 2560
			USSR	67. 643
	South Temperate Tropics	Africa	South Africa	27. 237
		Australasia	Australia	48. 275; 59. 564; 67. 660
		Africa	Malawi	34. 216; 35. 834; 36. 780
			Tanzania	48. 158
			Zaire	51. 196
			Zimbabwe	62. 126; 65. 598
		Asia	India (south)	64. 558

¹Published reports of *Armillaria* attack in forest plantations, woodlots, gardens, parks, roadsides, hedgerows, and farm shelterbelts. Includes ornamental nursery plants, trees established for shade or edible fruit supply (home or local, non-commercial use), and plants used to shelter production crops or provide green manure. References to trees

attacked within their natural distribution ranges (mainly North Temperate) are sometimes doubtfully included; it is not always clear whether these are planted or naturally seeded.

²As for Table 9.1.

TABLE 9.2b — *Armillaria* in planted non-coniferous (angiosperm) hosts, by country. (b) Species used in economic production (except forestry)^{1,2}

Crop	World zone	Continent	Country (and region)	References ²
Avocado (<i>Persea</i>)	North Temperate Tropics	America (North) America (South)	USA (Calif.) Ecuador	35. 707; 49. 630 (?); 56. 907; 66. 1868 60. 435
Banana	North Temperate South Temperate Tropics	America (North) Africa Australasia Africa	USA (Fla.) South Africa Australia Kenya Malawi Tanzania Zimbabwe	32. 382; 42. 497 72. 1693 34. 356; 67. 1674 (?) 54. 141; 65. 2697a 76. 5091 (HA) 33. 552; 53. 324 62. 126
Berryfruit – cane (<i>Ribes</i> ; currant, gooseberry) – bramble (<i>Rubus</i> ; blackberry, logan- berry, raspberry)	North Temperate	America (North) Europe (Western) USSR Australasia	Canada (BC) USA (Wash., Ore.) USA (Calif.) United Kingdom Soviet Union (Krasnodar)	38. 49 23. 278; 44. 112; 45. 423 52. 24 24. 525; 53. 320 72. 4191
Cacao (cocoa)	South Temperate Tropics	Africa	Australia New Zealand Cameroon Ghana & Togo Ivory Coast Madagascar Nigeria Sao Tome & Principe Uganda Zaire Mexico	49. 528; 60. 327 42. 29 57. 383 24. 325; 25. 463; 27. 19, 659, 704; 28. 93, 565 36. 16 55. 107 69. 755c 26. 149; 80. 5680 24. 509; 26. 17; 74. 1931 (HA) 47. 235; 49. 31, 272 49. 328
Cactus (<i>Opuntia ficus- indica</i> ; edible fruit)	North Temperate	America (Central) America (South) Australasia	Brazil Colombia Papua New Guinea	39. 93 (?) 60. 15 52. 9
Cassava (<i>Manihot</i>)	Tropics	Europe (Western)	Italy (Sicily)	83. 3151
Chesnut (<i>Castanea</i>)		Africa	Tanzania	33. 552
<i>Cinchona</i> (quinine)	Tropics	Zaire		57. 308
		America (South)	Brazil	36. 278 (?)
				Refer Table 9.2 (a)
		Asia	Guinea	59. 94
			Zaire	44. 431; 46. 45, 154; 51. 196
			Peru	55. 675
			Indonesia (Java, Sumatra)	23. 9; 24. 189; 25. 79; 28. 308; 30. 161; 31. 298; 37. 160; 39. 578
Citrus fruit (grapefruit, lemon, lime, orange, tangerine etc.)	North Temperate	Africa	Libya Morocco Tunisia	60. 658 64. 3222 33. 302
		America (North)	USA (Calif.)	26. 358; 30. 766; 32. 40; 41. 160, 360; 45. 225= 366; 49. 630; 51.

TABLE 9.2b — (Continued)

Crop	World zone	Continent	Country (and region)	References ²
Coffee	Temperate	Europe (Western)	USA (Fla.)	608; 54. 79; 55. 366, 641; 64. 520; 68. 1886; 69. 469; 70. 3661; 71. 1224d; 74. 2805 (HA); 77. 1943; 80. 5143, 5144
			Cyprus	31. 99; 32. 365; 42. 486, 497; 48. 279; 72. 1495
			France (incl. Corsica)	32. 696
			Greece (Crete)	56. 447; 86. 719
			Italy (incl. Sicily)	39. 672
			Malta	36. 213; 85. 4323; 88. 196
			United Kingdom	34. 81; 35. 618; 36. 780
			Yugoslavia	81. 6692 (HA)
				55. 297
	South Temperate	Australasia	Australia	23. 354; 27. 101; 33. 142; 36. 280; 37. 451; 42. 440; 44. 296; 46. 558; 47. 74, 337; 49. 453; 53. 175; 62. 151
				85. 2544
	Tropics	Africa	Kenya	33. 10
				38. 162; 39. 794; 40. 143
	Tropics	Africa	Malawi	37. 454
			Indonesia (Java)	55. 86
			General	54. 537
			Cameroon	67. 329; 69. 5; 70. 918
			Central African Rep.	59. 94; 63. 612
			Ethiopia	50. 99
			Guinea	26. 299 (?); 30. 31 (?); 60. 228; 73. 2278
			Ivory Coast	32. 699 (?); 34. 506 (?); 55. 107, 451; 58. 408; 63. 683; 64. 2914
			Kenya	28. 239; 62. 7
			Madagascar	72. 8a
			Malawi	59. 745 (?); 80. 4618
			Mauritius	33. 201; 34. 114; 36. 261; 51. 509
			Sao Tome & Principe	23. 409; 24. 509; 28. 701; 33. 422
			Tanzania	62. 761
			Uganda	39. 452
			Zimbabwe	56. 423
			Indonesia (Java)	27. 19
			Papua New Guinea	
			Ghana	
<i>Cola acuminata</i> (edible nut)	Tropics	Africa		
Cork (<i>Quercus suber</i>)	North Temperate	Europe (Western)	France	23. 431
			Italy (Sardinia)	64. 845
			Portugal	72. 4380 (?)
Cotton	Tropics	Africa	Zaire	49. 31
Fig (<i>Ficus carica</i>)	North Temperate	Africa	Algeria, Morocco, Tunisia	24. 88
		America (North)	USA (Calif.)	26. 37 (?); 48. 372
		Europe (Western)	France	47. 328; 82. 4011; 86. 2438, 5626
Flower production	North Temperate	Europe (Western)	France	Refer Table 9.2 (a)
Geranium/Pelargonium (oil source; see also Table 9.2a, Zaire)	Tropics	Africa	Kenya	56. 358
			Tanzania	51. 79
General	Tropics	Africa	Tanzania	36. 746
Grapevine (<i>Vitis</i>)	North Temperate	America (North)	USA (Fla., Missouri)	25. 585; 27. 460
			USA (Calif.)	51. 402; 64. 520; 73. 7573 (HA); 80. 1097 (SF), 9620 (PB)

TABLE 9.2b — (Continued)

Crop	World zone	Continent	Country (and region)	References ²
Guava (<i>Psidium</i>)	Temperate	Europe (Western)	Austria	81. 1114 (HA)
			Belgium	57. 86; 64. 1512v
			France	25. 525 (?); 27. 563, 586; 30. 360 (?); 38. 653; 59. 118 (?); 60. 767; 61. 507; 82. 4011, 4359; 86. 2211, 2438, 2441
			Greece	55. 706
			Italy	36. 774; 46. 436; 56. 658
			Spain	34. 745; 36. 75, 541; 53. 419
			Switzerland	56. 415; 76. 3131 (HA)
			Bulgaria	25. 460
			USSR	64. 1535m; 77. 3152
			Soviet Union (western, Georgia)	83. 3159
Hazelnut (<i>Corylus</i>)	Temperate	America (South)	Brazil (southern)	27. 101
			Australasia	30. 159; 42. 497
Hops (<i>Humulus</i>)	Temperate	Africa (North)	Australia	66. 700d
			USA (Fla.)	48. 165
Hydnocarpus anthelmintica (medicinal oil)	Temperate	America (North)	Malawi	85. 4520
			USA (Oreg.)	26. 278
			USA (Oreg.)	49. 593
			Italy	60. 210
			United Kingdom	36. 478, 605; 37. 822; 40. 364; 43. 39; 44. 2
			USA (Oreg.)	60. 327; 63. 137
Kiwifruit (<i>Actinidia</i>)	Temperate	Europe (Western)	Australia	60. 327; 63. 137
			Africa	49. 271
			Zaire	49. 271
Lavender (<i>Lavendula</i> ; perfume)	Temperate	America (North)	USA (Calif.)	72. 2721
			Europe (Western)	86. 2438 (?)
			Australasia	71. 3066
Litchi (<i>Litchi</i> ; edible fruit)	Temperate	Europe (Western)	New Zealand	71. 3066
			France	34. 99
Loquat (<i>Eriobotrya</i>)	Temperate	Europe (Western)	United Kingdom	39. 724
			USA (Fla.)	42. 497 (?); 56. 781;
Macadamia Nut	Tropics	America (North)	USA (Calif.)	62. 618 (?)
			USA (Calif.)	27. 175; 49. 630 (?)
Mangel (<i>Beta</i> ; cattle food)	Temperate	Africa (North)	Tanzania	38. 15
			Zimbabwe	68. 2588
Mango (<i>Mangifera</i>)	Temperate	Europe (Western)	Canada (New Bruns.)	36. 632
			Ghana, Uganda, Zimbabwe	Refer Table 9.2 (a)
Mulberry (<i>Morus</i>)	Temperate	Europe (Western)	France	25. 201; 27. 567
			Italy	29. 207; 30. 213
		Europe (Eastern)	Hungary	86. 781
			USSR	46. 17

TABLE 9.2b — (Continued)

Crop	World zone	Continent	Country (and region)	References ²
Oil palm (<i>Elaeis guineensis</i>)	South	Australasia	Kirghiz., Tadzhik. ?)	27. 101
			Australia	
	Tropics	Africa	Zaire	47. 235; 49. 31, 272; 50. 236, 292; 51. 155, 512; 57. 513
			France	24. 348; 82. 4011; 86. 1420, 2438
Olive	North	Europe (Western)	Italy	46. 492; 51. 235; 56. 658; 62. 358; 76. 1641 (HA)
			Spain	46. 508
	Tropics	Africa	Malawi	31. 707
			Kenya	48. 483; 71. 5b
Papaya (papaw)	Tropics	Africa	Tanzania	48. 483; 50. 145
			Australia	27. 101
	South	Australasia	Zimbabwe	65. 598
			USA (Georgia)	71. 294
Passiflora spp. (passionfruit, granadilla)	North	America (North)	USA (Calif.)	48. 372 (?); 49. 630 (?)
			Canada (BC)	23. 304; 26. 146
	Temperate	America (North)	USA (Wash., Ore.)	24. 89; 26. 746; 30. 212
			USA (Calif.)	23. 394; 32. 40; 25. 21; 26. 37; 34. 552; 40. 24; 48. 372; 64. 520 (?), 2855; 72. 1631
Pecan (<i>Carya illinoensis</i>)	North	America (North)	USA (Louis., Fla.)	41. 169; 42. 497
			France	23. 431 (?); 59. 125; 86. 2438
	Temperate	Europe (Western)	German Fed. Rep.	35. 677 (?); 71. 1867 (?)
			Italy	74. 2033 (HA)
Persimmon (<i>Diospyros</i>)	North	America (North)	Malta	36. 780; 38. 589
			Netherlands	51. 420
	Temperate	Europe (Western)	Spain	34. 745 (?); 36. 75 (?), 541 (?); 42. 338
			Switzerland	50. 443
Pome fruit (<i>Malus</i> , <i>Pyrus</i> ; apples, pears)	North	America (North)	United Kingdom	24. 259; 26. 278; 37. 822; 53. 320; 54. 91; 60. 178 (?); 70. 1426
			South Africa	37. 784 (?)
	South	Africa	Chile	69. 2282
			Australia	23. 353; 25. 399 (?); 26. 105; 27. 101; 28. 304 (?); 35. 451 (?); 45. 318 (?); 56. 613 (?); 60. 327; 62. 158; 67. 2775
Rubber (<i>Hevea</i>)	Tropics	Africa	Kenya	51. 309
			Tanzania	48. 224
	Tropics	Africa	Zaire	51. 196
			Zimbabwe	36. 705; 38. 46; 66. 2a
Rubber (<i>Hevea</i>)	Tropics	Africa	Cameroon	66. 1166
			Central African Rep., Chad, Congo &/or Gabon	53. 507
	Tropics	Africa	Congo	64. 3003
			Nigeria	64. 3003, 3172; 66. 1166
Rubber (<i>Hevea</i>)	Tropics	Africa	Uganda	24. 509
			Zaire	47. 466; 48. 123, 382; 49. 271; 50. 236, 292; 51. 512; 54. 413; 55. 583; 56. 925; 57. 308; 61. 486

TABLE 9.2b — (Continued)

Crop	World zone	Continent	Country (and region)	References ²
Stone fruit (<i>Prunus</i> ; almond, apricot, cherry, peach, plum, etc.)	North Temperate	America (North)	Canada (BC, Ont., Queb.)	26. 146; 47. 429 (?); 75. 2151 (HA)
			USA (Wash., Ore.)	26. 746
			USA (Calif.)	25. 681; 26. 37; 31. 323; 34. 552; 36. 518; 40. 24; 41. 161; 45. 453; 46. 446; 48. 372; 49. 630; 52. 68; 53. 24; 54. 36; 64. 520 (?), 2855; 72. 4174; 77. 1943
			USA (Wisc., Ill., Mich.)	23. 481; 54. 733; 88. 4191 (FA)
			USA (Mary., Nth Carol., Sth Carol., Georg., Fla.)	30. 159; 41. 68, 562; 42. 497; 44. 25; 53. 682; 54. 434; 55. 603; 61. 370; 62. 398; 63. 618; 69. 1842
		Europe (Western)	France	23. 431 (?); 26. 304; 27. 563 (?); 30. 116, 465; 32. 791; 49. 527; 50. 265; 54. 161; 56. 109, 305; 82. 4011, 4359; 86. 2211, 2438, 2441; 87. 9220 (HA)
			German Fed. Rep.	35. 677 (?); 71. 1867 (?); 73. 63 (HA)
			Italy	34. 706; 56. 658; 63. 562; 68. 2215
			Netherlands	48. 244
			Spain	34. 745 (?); 36. 75 (?), 541 (?)
			United Kingdom	28. 647; 37. 822; 60. 178 (?)
			Hungary	47. 344; 48. 140; 86. 781
		Europe (Eastern)	Yugoslavia	86. 808
			South Africa	27. 237; 37. 784 (?)
	South Temperate	Australasia	Australia	25. 399 (?); 28. 304 (?); 35. 451 (?); 45. 318 (?); 47. 285; 48. 27; 56. 613 (?); 65. 1354g; 67. 2775; 73. 2099f
			Kenya	37. 796 (?); 51. 309; 58. 136
	Tropics	Africa	Zimbabwe	36. 705; 38. 160
			USA (Wash., Ore.)	29. 727; 31. 163; 32. 727; 39. 402; 45. 423
			USA (Calif.)	61. 617
			United Kingdom	27. 650
Strawberry (<i>Fragaria</i>)	North Temperate	America (North)		
Sugar cane (<i>Saccharum</i>) Tea	Tropics	Africa	Tanzania	33. 552
	North Temperate	Asia	India (northeast)	40. 369; 83. 3975; 85. 2155
	Tropics	Africa	Kenya	53. 513 (?); 58. 512; 60. 214; 61. 73, 723; 76. 10851 (HA)
			Malawi	28. 275; 29. 202; 33. 10; 34. 216; 35. 14; 36. 780; 37. 209, 564; 40. 311; 49. 200; 74. 8119 (HA); 81. 3935
			Mauritius	52. 538
			Mozambique	50. 89
			Tanzania	36. 261; 53. 513 (?); 55. 350
			Uganda	24. 509; 29. 756; 37. 838
			Zaire	49. 272; 57. 309 (?); 60. 440
			Zimbabwe	59. 295; 65. 598
		Asia	India (south)	55. 489; 60. 123; 64. 558; 66. 595b; 76. 8835 (HA)
			Indonesia (Java, Sumatra)	23. 9; 24. 5, 64, 611;
			Malaysia	26. 585; 31. 409; 38. 162, 202; 39. 579
				37. 657 (?)
			Sri Lanka	23. 295; 28. 745; 29. 469; 31. 275; 40. 678 (?)

TABLE 9.2b — (Continued)

Crop	World zone	Continent	Country (and region)	References ²
Tung (<i>Aleurites</i> ; oil)	North Temperate Tropics	Australasia	Papua New Guinea	56. 423
		America (North)	USA (Louis., Fla.)	37. 426 (?); 41. 169; 44. 504; 49. 365
		Africa	Malawi	40. 626; 49. 200; 51. 295; 53. 703; 62. 734
		Asia	India	50. 588 (?; see 55. 267)
Vegetables (carrot, parsnip, potato; also tomato; see elsewhere for cassava, mangel)	North Temperate	America (North)	Canada (BC)	37. 832
		Europe (Western)	Belgium	39. 724; 71. 460b
			United Kingdom	22. 357; 48. 462
		USSR	Soviet Union (Leningrad)	46. 316
Walnut (<i>Juglans</i>)	South Temperate	Australasia	Australia	27. 101; 33. 142; 34. 257; 37. 118
	North Temperate	America (North)	USA (Ore.)	24. 89; 42. 310; 49. 94; 51. 594; 52. 463; 59. 39
			USA (Calif.)	26. 37; 34. 552; 45. 453; 48. 103, 372
		Europe (Western)	France	22. 35, 77; 24. 179; 25. 201, 577; 26. 526; 27. 200, 426, 563, 586; 28. 686; 32. 95; 34. 366 (?); 36. 763; 72. 4403 (?); 84.4723 (FA)
			Italy	46. 427
		Europe (Eastern)	Bulgaria	76. 6817 (FA); 77. 871 (FA), 4716
			Czechoslovakia	27. 6
			Hungary	48. 140; 86. 781
	South Temperate	Australasia	Australia	54. 610

¹Published reports of *Armillaria* attack to planted trees, shrubs, or herbaceous species used as commercial food crops or for processed products (except timber or pulpwood).

²As for Table 9.1.

Modeling the Dynamics, Behavior, and Impact of Armillaria Root Disease

Charles G. Shaw III, Albert R. Stage, and Peter McNamee

Information on the ecological, biological, and pathological attributes of *Armillaria* spp. and the root disease they cause comprises the major portion of this book. Integration of this material, particularly as it relates to the portrayal of disease dynamics and the quantification of disease impacts, would markedly enhance its utility for foresters, orchard managers, and scientists. Models can accomplish this objective, and some have been developed for root disease caused by *Heterobasidion annosum* (Fr.) Bref. (Alexander and others 1985, Pratt and others 1989) and *Phellinus weirii* (Murr.) Gilbn. (Bloomberg 1988).

This chapter describes how information on Armillaria root disease has been used to develop a predictive model of disease dynamics, behavior, and impact. Foresters currently make decisions about root disease management using their mental model of the disease process in the affected area as a guide to select treatment alternatives for the land. The process of building a predictive model combines existing data and the key features of the mental models of several knowledgeable forest managers and scientists in a set of mathematical equations. By pooling and structuring the knowledge of many, we should have a better model for individual stand management as well as for overall forest planning than would be assembled by any single manager or scientist. An important benefit of the model-building process is a highlighting of our still inadequate understanding of many biological aspects of Armillaria root disease, increased knowledge of which is necessary to improve management.

Pathologists have a wealth of information about *Armillaria* spp. and the root disease they cause. However, even when these data are published they frequently are not available to managers in a form that directly assists decision making. Because pathologists have the best biological understanding of root disease dynamics as well as the limitations of available data, it is imperative that they define the biological assumptions necessary to develop a predictive model. If research pathologists

diligently perform this role, then the resulting model not only becomes a tool of immediate use to managers, but also becomes a quantitative description of a series of hypotheses about root disease dynamics, behavior, and impact. As such, it can aid scientists in identifying serious data gaps and thus help to define and prioritize research needs.

Scientists trained in the research process may find development of a management-oriented model troublesome because professional judgement, rather than statistically analyzed data, often becomes the only, or at least primary, basis for a generalized assumption that can markedly influence the outcome of a model prediction. The traditional researcher is far more comfortable with the model of a scientific paradigm where behavior is judged at levels that are often far removed from the decision criteria that are required of a predictive model for management. Consequently, knowledge gaps can be left to future research as no immediate opportunity exists for application of the model. Forest managers who routinely encounter stands severely impacted by root diseases are desperate for tools to deal with these complex and damaging problems. Thus scientists, who best understand these problems, even if that understanding comes primarily from their professional judgements and experiences, can no longer take a laissez faire, hands-off approach to management-oriented modeling.

This chapter describes the integration of our current understanding of Armillaria root disease dynamics and the damage the disease causes in various conifer ecosystems in western North America (see chapter 8) into a predictive model for management use in silviculture and forest planning (Stage and others 1990). The hypotheses or assumptions that underlie the quantitative relationships contained in the model are discussed and referenced to information presented elsewhere in this book. In addition, direction is provided to indicate how model users (both managers and scientists) can examine alternative hypotheses about the dynamics and behavior of Armillaria root disease.

The process used to build the Western Root Disease Model (Brookes 1985, Eav and Shaw 1987, Shaw and others 1985) can serve as a prototype for modeling the dynamics and behavior of *Armillaria* root disease in other forest ecosystems or orchards.

History and Structure of the Western Root Disease Model

Recognizing the serious economic impact of annually losing 6.8 million cubic meters of timber in the Western United States to root diseases (Smith 1984), the USDA Forest Service initiated a project to develop a root disease model (Brookes 1985). The protocols of Adaptive Environmental Assessment, as outlined by Holling (1978), were used to develop the Western Root Disease Model. In this procedure, serial workshops allow various experts in disease recognition, biology, and management to meet with potential model users for short periods of intense interaction. Through the direction and assistance of model coordinators, they develop a conceptual model of the problem and possible management actions to mitigate damaging effects (Brookes 1985). The coordinator is then responsible for converting this information into a working, predictive model that is further refined at subsequent workshops through additional input from specialists and potential users. The process itself is not new, but it creatively extends the scientific method from the individual investigator to a corporate surrogate (Walters 1986).

A recognized strength of the procedure is that it gives ownership of the final product, and thus a desire to have a quality item produced in a timely manner, to all who were involved with its development. Also, because the model building is cooperative, scientists can appreciate the need to provide managers with the best current understanding of root disease spread and impact, and managers can recognize the critical uncertainties in our knowledge of root disease biology and the need for further research.

The model was developed as a tool to aid foresters with overall, forest-level planning and with the design of silvicultural treatments in individual stands affected by root disease. The model can project the effects of various levels of *Armillaria* root disease on future stand composition and structure which, for timber purposes, can be converted into volume losses. The latter is particularly significant since current expectations of timber yields over the next decade from certain forest areas in western North America may be over-estimated by 50% because effects of *Armillaria* root disease have not been considered.

Even with the wealth of available empirical information, relationships that are appropriate for modeling

disease behavior at the stand level need to be postulated. In modeling the dynamics and behavior of *Armillaria* root disease in forests of western North America, we found that the available information for specific components ranged from virtually no hard data to two or more conflicting data sets or opinions. Therefore, it became critical to document assumptions made during the modeling process because: (1) if model performance is questionable in certain areas, then the assumptions can be checked to see if they help to explain the concern; (2) if new information becomes available, then the current assumptions can be appropriately modified; and (3) if theory or concepts change in areas where little empirical information exists, then documentation of initial assumptions is necessary to consider any possible changes.

The model dynamically represents the spatial and temporal epidemiology of pathogenic *Armillaria* species or *P. weirii* (McNamee and others 1989, Stage and others 1990). It can project up to 40 growth cycles of stand development, normally of 10 years each, and operate in stands up to 100 ha. The three main components or submodels are root disease per se, "other agents," and an interface to a vegetation model (fig. 10.1). The root disease submodel provides the status and spread of

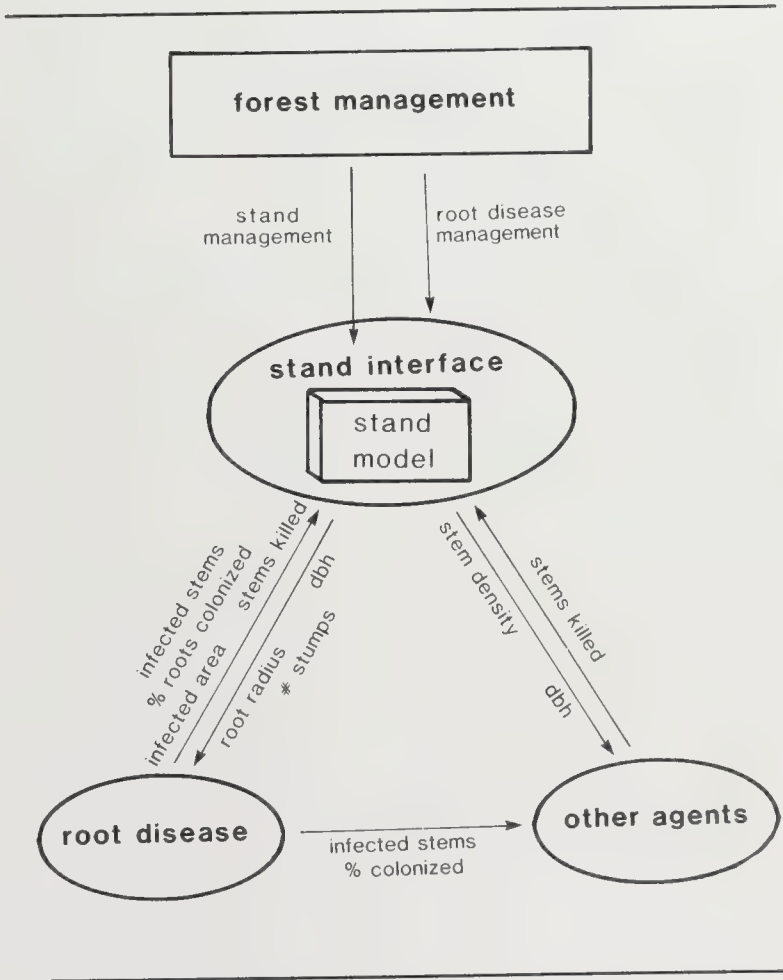


FIGURE 10.1. — Relationship among the three models of the Western Root Disease Model.

root disease and contains a Keyword mechanism to modify relationships to meet particular conditions (Stage and others 1990). This feature allows the user to explore alternative hypotheses concerning root disease dynamics. The "other agents" submodel simulates the effects of wind-throw and three types of bark beetle behavior. This submodel is important because it structures the interactions between root diseases and other mortality agents that can be important and damaging factors in forests of western North America (Shaw and Eav 1991). The stand-interface submodel links the stand-development model, to which the Western Root Disease Model must be attached, currently Prognosis (Stage 1973, Wykoff and others 1982), and the root disease and "other agents" submodels.

Critical Model Relationships and Associated Assumptions and Hypotheses

Spatial Resolution

The Western Root Disease Model spans two levels of organization: individual trees and the aggregation of these individuals into stands. Within a stand, two strata are defined with respect to root disease. The first consists of areas that are clearly beyond the influence of currently diseased trees. The second stratum consists of a number of root disease centers, each of which contains infected trees, uninfected trees, and other inoculum sources such as infected stumps. The size and separation of areas in these two strata define the spatial resolution of the model.

Within each stratum, the actual spatial proximity of individual trees is not maintained. When rates of pathogen spread to uninfected trees are calculated, however, the individual trees in a sub-sample of the first stratum are assigned x-y coordinates according to whether the stand is of natural origin (a random distribution is assumed) or is evenly spaced as in a plantation.

Center Dynamics

The model addresses three important characteristics of root disease centers: the dynamics of infection and inoculum within root disease centers; the expansion of root disease centers; and the carry-over of root disease to a new stand following stand entry.

Inside Established Centers

Progression Within Single Trees

The relationship that describes how live root systems become infected, trees are killed, and infection spreads

in dead, infected roots (fig. 10.2) is a fundamental function of the model. This relationship was developed from the experiences and judgements of those who participated in model development. Chapters 4 and 5 provide background information relevant to these assumptions.

The relationship that describes the time between initial infection and death of a Douglas-fir tree on Douglas-fir habitat in the interior region of the Western United States is shown in fig. 10.3. This relationship is modified for other species and habitat types, but the hypothesis is that all trees react similarly to infection. The relationship represents, with some reference to published information (Hadfield and others 1986), the best professional judgement of the pathologists who participated in model development. They realized that, as modeled, the relationship may not be appropriate under situations of scattered mortality, a situation needing further research. For example, how is the percentage of a root system that is infected when a tree dies affected by *Armillaria* species, tree species, stress, etc? In recognition of these uncertainties, critical points of the relationship can be modified using the Keyword system (Stage and others 1990).

For example, one Keyword specifies the level of root infection at which trees die and allows users to vary the level for different tree species and sites. Another Keyword can be used to change the time-to-death for infected trees. A third Keyword allows users to modify infection and mortality dynamics by tree size.

A consensus of pathologists in western North America suggested the values in table 10.1 for the average portion of a root system that is colonized by *Armillaria* when a tree dies. Following tree death, the model

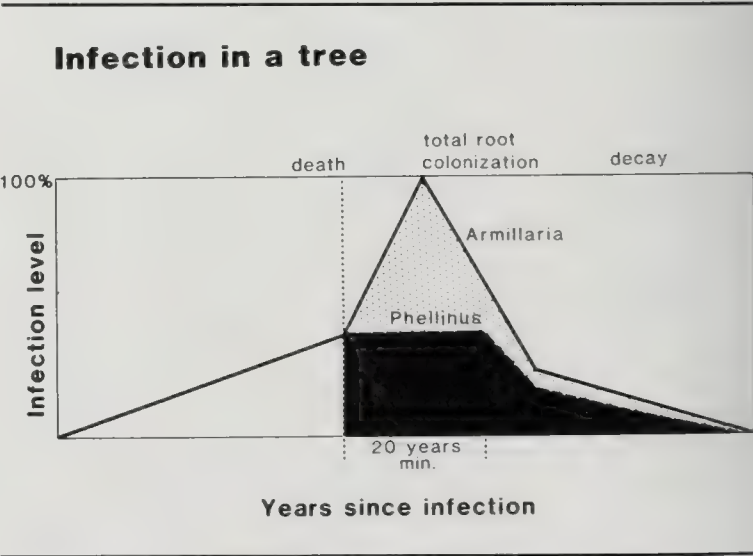


FIGURE 10.2 — Pattern of root pathogen spread and inoculum buildup and decline in a single tree root system.

infection levels causing death

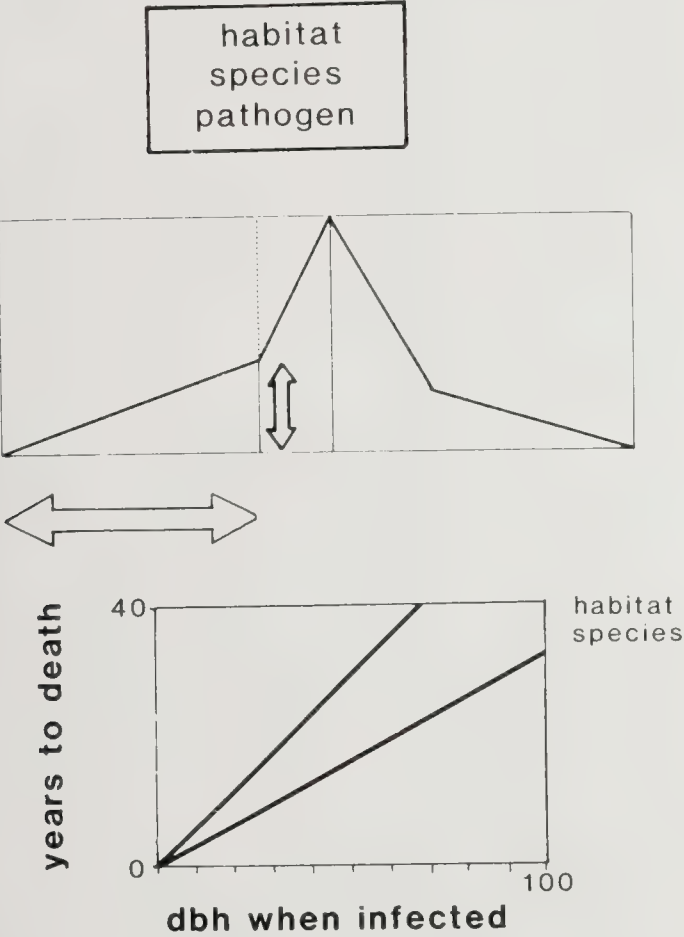


FIGURE 10.3 — Time required from infection by *Armillaria* to tree death for Douglas-fir on a Douglas-fir habitat type.

assumes that *Armillaria* colonizes all remaining portions of infected root systems within 5 years. Supporting evidence for this comes from Morrison (1981) and Shaw (1980).

The model assumes that dead trees or stumps can only become inoculum if, prior to their death or cutting, their root systems were already colonized to some degree with a pathogenic species of *Armillaria*. Even if a tree only has a small lateral lesion somewhere on its roots (Shaw 1980), its entire root system will, under this assumption, become inoculum within 5 years. Contrarily, trees not already infected at cutting, regardless of location, will not become inoculum. Even though this modeling assumption contrasts with certain hypotheses about the competitive saprophytic ability of *Armillaria* (see chapter 4, Garrett 1970), the model does provide sufficient inoculum for disease to progress in a manner judged to be reasonable by knowledgeable forest pathologists in western North America.

This assumption may be logical for modeling in coniferous forests of western North America. These forests show limited rhizomorph development by pathogenic species

TABLE 10.1 — Average percentage of root systems assumed to be infected at the time a tree is killed by root disease.

Tree species	Fungal Species	
	<i>Armillaria</i>	<i>P. weirii</i>
	(% root system infected)	
Douglas-fir	80	60
Pines	30	85
True fir	80	60
Hemlock	80	80
Spruce	75	65
Larch	00	75
W. redcedar	75	85

of *Armillaria* (Shaw 1980), and pathogenic lesions frequently occur on trees with little above-ground evidence of infection other than proximity to trees with obvious symptoms or signs of infection (see chapter 5). Perhaps the earlier assumptions on competitive saprophytic ability, developed primarily in the United Kingdom, need to be re-examined regarding current information on the pathogenicity of various *Armillaria* species and their relative in vivo abilities to produce rhizomorphs (see chapters 4 and 6).

In the model, how disease spreads through root systems of dead trees is independent of how the trees died, even though in reality the speed and mechanism of death may affect either the proportion of the root system actually colonized or the viability of resulting inoculum. This assumption relates to a fundamental research need regarding *Armillaria* root disease: the importance of, and mechanisms for, interaction of root diseases with other agents (both biotic and abiotic) of stress (see chapters 7 and 8; Shaw and Eav 1991).

The maximum lifespan of effective inoculum also may be affected by habitat type or other environmental parameters; however, users can modify these parameters. As modeled, the lifespan of effective inoculum is assumed to be a function of stump size and species, with rather rapid deterioration after maximum build-up (fig. 10.4). Species are grouped into heartwood (Douglas-fir, pines, and larch) and nonheartwood types (true firs, hemlocks, and spruce), with the latter decaying more rapidly. Inoculum is assumed to decay at a rate that reduces the radial extent of infected root systems by 75% during the first one-third of their lifespans. The remaining infected roots are assumed to decay at a steady rate over the remaining two-thirds of their lifespan. The pattern of inoculum decay is undoubtedly influenced by habitat type, tree rooting habit, temperature, moisture, and other abiotic factors not captured in the model but discussed in chapters 4 and 7.

Spread from Tree to Tree

Pathogen transmission to adjacent, living trees is modeled as a probabilistic process of two parts. First, an uninfested root system overlaps an infested system; and second, the pathogen will be transmitted given that the root systems overlap. The latter probability is controlled by a species-dependent Keyword. The first probability is calculated by simulation on a map which plots individual trees. Their spatial distribution is modeled as random (Poisson) for natural regeneration or a lattice for plantations, and can be changed by the user during the simulation. Kellas and others (1987) also suggest modeling tree distribution in Australian mixed species eucalypt stands with a Poisson distribution modified for stumps colonized by *Armillaria*.

Pathogen transmission via rhizomorphs is not explicitly modeled though one can change infection probabilities. Thus, increasing the probabilities of root system overlap, or pathogen transmission given root overlap, could be used to accommodate the activity of rhizomorphs where they are considered important agents of infection (see chapter 4).

Quantity of Inoculum

The quantity of inoculum available in a stand is estimated from the area occupied by infected roots. This

area is determined by the relation of root extent to tree diameter and species, with rooting patterns assumed to be circular. If rhizomorph networks extend the influence of inoculum beyond the actual root systems boundaries (see chapter 4), then the areas could be increased. This action was considered to be unnecessary in forests of western North America because of limited in vivo rhizomorph production by the primary pathogenic species (see chapters 4 and 6). As described above, the size of these areas declines with time to represent the decay of root systems after tree death.

We know these assumptions have inherent inaccuracies and simplifications. For example, the density of roots is not uniform across a radius drawn outward from a stump, but decreases with distance from the stump. And, of course, trees, particularly when growing on slopes, do not have roots with a uniform, circular distribution. However, the important attribute is area, which is only slightly different for an ellipse than for a circle. A more detailed representation of actual root system geometry would have considerably complicated the model, with a limited likelihood of improving predictions.

Expansion of Centers

The simulation for enlarging infection centers has two main components: estimating the average rate of enlargement and translating that rate into a new stand area encompassed by root disease.

Rate of disease spread into uninfested area is simulated by a subroutine with enhanced spatial resolution. It maps a sample of the trees still outside the infection centers onto a smaller square area within which trees are assigned x-y coordinates. Then, the same relations that describe increases in area occupied by infected roots (fig. 10.2) and the probability of transmission, given that the root area of an uninfested tree overlaps that of a diseased tree, are used to estimate the time required for the disease to propagate across the width of the map. Width of map divided by the estimated time defines the radial spread rate of disease centers. The spread rate is thus not an input parameter but is calculated by the model. As such, it provides a means to gauge model performance as data on rates of infection center enlargement are available (see chapter 8). As an option, one can override this model function and input a static spread rate.

When this radial increment is added to the radius of each existing infection center, some centers may overlap. However, the new area of infection is calculated after adjusting for overlaps. The increase of infected area divided by the previously uninfested area pro-

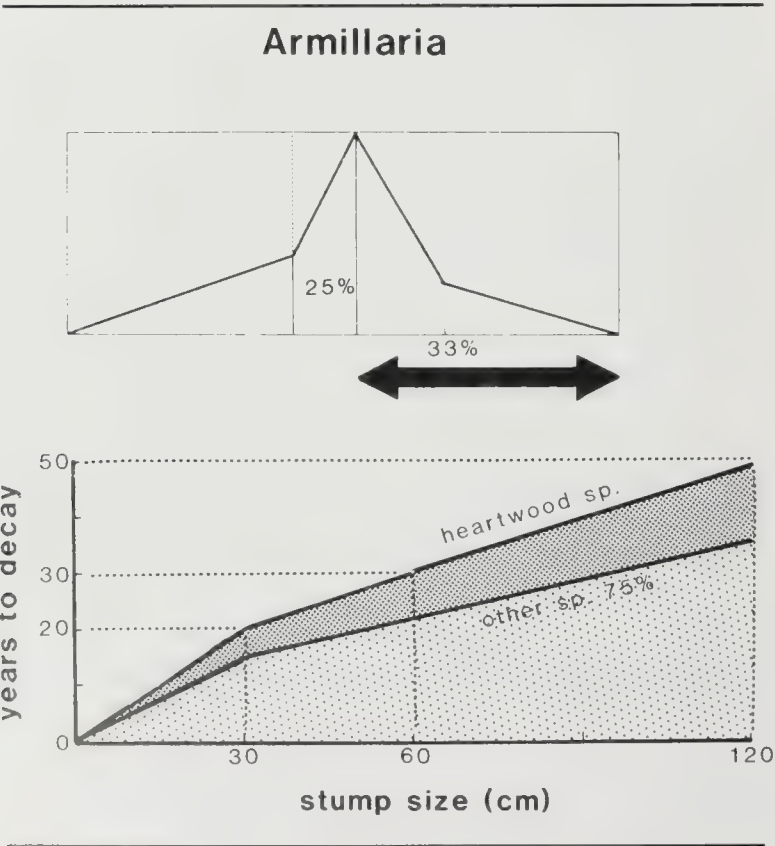


FIGURE 10.4 — Lifespan of *Armillaria* inoculum for trees with and without heartwood; see text for detailed description.

vides a proportion for moving trees from the uninfected tree inventory to the infected tree inventory.

Carryover to Regeneration after Harvest

How root disease centers are affected by clearcutting and regeneration of a new stand is poorly understood. The modelers considered three different “carryover” scenarios: (1) root disease centers from the former stand cease to exist after clearcutting, and root disease in the new stand arises in a small number of new centers located within previously infected areas; (2) root disease centers from the former stand retain their integrity, and, as the new stand matures, these centers enlarge, starting at their old boundaries; and (3) after a clearcut and regeneration, root disease centers form around certain individual pieces of inoculum throughout the area affected in the former stand and these centers gradually expand and coalesce. These three scenarios actually form a continuum that depends on inoculum density and the probability of a piece of inoculum initiating a new center that is capable of expanding.

New disease centers have equal probability of occurring anywhere root disease occurred in the previous stand and no probability of occurring elsewhere. This assumption implies that all disease in the previous stand was noticeable and detected in the stand examination (see chapter 5) and that spores do not initiate new centers. We realize that the latter event must occur at some time (see chapter 9). However, for *Armillaria* root disease in western coniferous forests, in contrast to root disease caused by *H. annosum* in these same forests (Shaw and others 1989b), its occurrence seems to be infrequent enough that it can be ignored for stand-level modeling purposes—particularly when modeling stands that are already infected. Information presented in chapters 7, 8, and 9 supports this view.

A ring of root systems around the outside of each disease center represents trees that have just been infected. When these trees are cut, the prompt colonization of their entire root systems by the fungus causes disease centers to expand rapidly. In the model, the mean diameter of all root systems in the stand at the time of the cut is the distance by which radii of disease centers increase. Evidence for such action is found in Morrison (1981) and Shaw (1980). A major unknown is how far root disease actually does “jump out” from the recognized, above-ground edge of a center after clearcutting. cursory examination of model behavior suggests that this is a sensitive parameter and thus it can be controlled by use of a Keyword. This feature of the model was most useful in preliminary work on adapting the Western Root Disease Model to represent root disease caused by *H. annosum* (Shaw and others 1989b).

Representation of Management Actions

Inoculum Removal

The Western Root Disease Model can simulate inoculum removal through “pushing” or removing infected stumps and their root systems (see chapter 11). This option can be requested in a specific year, with a factor specifying the efficacy with which roots are removed and the minimum diameter of dead trees and stumps to be removed. Even though this practice is an accepted management alternative in certain stands (Roth and others 1977), it is not universally applicable (Wargo and Shaw 1985).

Silvicultural Treatments

Regeneration systems ranging from single-tree selections to clearcutting can be simulated. Besides harvesting existing trees, new stands can be introduced following site preparation either by natural regeneration or by planting with species selected for disease resistance (see chapter 11). Likewise, particular species can be favored during thinning or during other partial stand harvests.

A full range of treatment alternatives may be considered when regenerating diseased stands, depending on economic constraints and stand management objectives. The most frequent approach to managing root disease problems in timber stands throughout western North America is regeneration to site-suited tree species that are disease tolerant (Hadfield and others 1986, Morrison 1981). The model can be used to compare the effects of various approaches. For example, the following options are among the many that may be compared and considered:

- No action—leave the stand “as is,” but recognize presence of root disease.
- A clearcut, seed-tree cut, or shelterwood cut followed by natural regeneration. The mixture of species in the resulting regeneration will depend on the habitat type.
- Overstory removal to leave an understory of tree species that might be disease susceptible, disease tolerant, or a mixture of the two.
- A clearcut with stump removal followed by planting of a disease-susceptible but otherwise preferred species.
- A clearcut without stump removal followed by planting of a disease-susceptible but otherwise preferred species. Comparison to the preceding option provides an estimate of the control value of stump removal (see chapter 11).
- A base simulation, without invoking the Western Root Disease Model, of the Prognosis model for

stand development, perhaps followed by planting of a preferred but disease-susceptible tree species. These scenarios represent "control" simulations for the Western Root Disease Model.

Besides aiding management decisions, gaming with the model by preparing such scenarios can help scientists identify research needs relating to treatment alternatives. For example, the efficiency of stump removal (i.e., the proportion of inoculum removed) is a sensitive parameter in the model which suggests that carryover of root disease as a function of stump-removal efficiency is an important research area, particularly since little information exists on the topic.

What Data are Required?

The model is designed to start with sample inventories of actual stands. For example, the compartment examination procedure described by Stage and Alley (1972) and in the Forest Service Handbook for Region 1 (USDA Forest Service 1986) can supply the necessary stand data if it is augmented to include stumps infected with root disease (see chapter 5).

Besides the customary tree-size attributes, the model uses information on the frequency of tree infection by root pathogens. This value can be compiled by the model from disease status codes of the individual sample trees, or supplied by the user from an overall estimate based on an independent sample of the stand. The Western Root Disease Model also uses data on the area of the stand and the sizes and distribution of disease centers to initiate the simulation. The user may specify a total area in root disease and the number of centers. In this case, the model randomly locates root disease centers throughout the stand. Initially, each center will be of equal size, calculated as the total area in root disease divided by the number of centers. The alternative is to provide a list of root disease centers with X and Y coordinates and a radius for each center.

The model can start from bare ground by planting, by invoking the Regeneration Establishment component of the Prognosis model for stand development (Fergu-

son and others 1986), or from the stand description contained in the list of trees sampled in the inventory.

Conclusions

We believe that the Western Root Disease Model provides a workable framework for others to consider when modeling the behavior of *Armillaria* root disease in orchards or other forest situations. The current model should continue to improve as new information becomes available. The model is currently undergoing an analysis of its sensitivity to changes in the various parameters that control it and thus the assumptions and hypotheses under which it was developed (Marsden, unpubl.). We believe that the items to which the model is the most sensitive (longevity of inoculum and the quality, quantity, and type of input data) are the ones where additional resources could best be put to improve model performance. Thus, a list of research needs relevant to improving model reliability can be generated through a structured sensitivity analysis.

If the procedure we have outlined is used in model development, then it is critical that participants in the process represent a cross section of interested and knowledgeable scientists, managers, and administrators. Furthermore, it is paramount that scientists be willing to extrapolate beyond the limits of available data to help meet existing management needs. In so doing, however, they must insist that all extrapolations and assumptions are thoroughly documented. Also, such disease models need to be developed so that they can function in concert with existing models that may predict other stand or orchard attributes such as yield or watering regimes.

Based on how well users have accepted the Western Root Disease Model for both short-term, site-specific management decisions and long-range applications in planning, we strongly encourage others to pursue this avenue for transferring technology on *Armillaria* root disease dynamics into a useable tool for managers. We also contend that the process of doing so will help scientists clarify the current state of knowledge and help to focus management-oriented research needs.

Avoiding and Reducing Losses from Armillaria Root Disease

Susan K. Hagle and Charles G. Shaw III

As the forest and agricultural land base is increasingly utilized, careful stewardship of remaining productivity becomes increasingly important. *Armillaria* epiphytotics can not only cause marked reductions in fruit and fiber production (see chapters 8 and 9), but they may also carry high economic, social, and ecological costs for control. In some forest settings, properly applied cultural control methods are efficient and effective. But for many crops, we lack convenient, cost-effective methods for control. In fact, it has been said (Schütt 1985) that while our biological knowledge about *Armillaria* has increased markedly since the time of Hartig, the efficiency of control measures, with some exceptions, has not improved very much. However, advances in our ability to identify species accurately (see chapters 1 and 2), determine their relative pathogenicities (see chapter 6), and model the disease process (see chapter 10) provide us a sharper image of disease problems, and should allow a more systematic evaluation of control options.

In this chapter, we examine various approaches and techniques for control and avoidance of *Armillaria* root disease in forests, orchards, and amenity plantings. These include use of resistant species, avoidance of hazardous sites, cultural manipulation, chemical application, biological methods, and integrated biological methods. Chapter 9 contains related material on management practices in plantations that can reduce losses from *Armillaria* root disease.

Armillaria species cause three types of disease in indigenous forests (see chapter 8). In one type, tree and shrub species are attacked and killed by an aggressive, primary pathogen (Filip 1977, Gibson 1960, Kile 1981, MacKenzie and Shaw 1977). In another type, the fungus lives primarily in chronic infections it causes on roots that may but seldom become aggressive. The third type causes butt rot that may or may not be related to other disease types (see chapters 5 and 6).

The first disease type often requires radical measures to effect control. The other two types may cause little dam-

age if stand management maintains the resistance or tolerance of infected trees. In these latter two, a shift in the balance between the host and the pathogen induced by stresses such as drought, insect attack, other diseases, or anthropogenic activities can allow the fungus to expand and kill the host (see chapter 7).

The pathogenic behavior of *Armillaria* species in plantations, orchards, and amenity plantings also ranges from aggressive to benign. Control options may, however, differ from those that are feasible in indigenous forests, and they also may be more costly; however, the higher commodity values may offset higher costs (see chapter 9).

The type of root disease expression (see chapter 5) and the extent of damage are related to species and genotypes of *Armillaria* (Shaw and others 1981, Guillamin and Lung 1985, Rishbeth 1982, Kile and Watling 1988, Roll-Hansen 1985, Intini 1989a), inoculum characteristics (see chapter 4), inherent host resistance or tolerance (Thomas and Raphael 1935), host adaptation to site (Intini 1989a, Singh and Richardson 1973), stand structure and species composition, management history, and site factors which directly affect the pathogen (Redfern 1978, Blenis and others 1989; see chapter 6).

Where *Armillaria* acts as a secondary pathogen on plants that are predisposed in some way, control efforts should focus on the predisposing condition (see chapter 7). This problem becomes especially acute in situations such as those created by atmospheric deposition or photochemical oxidant injury, which are not only difficult to document but also difficult to control for societal reasons. In such cases, we could find ourselves treating symptoms at great expense with little benefit.

Where *Armillaria* is a primary pathogen, infection often leads to rapid death even if the plants were vigorous prior to attack. This distinction in pathogen behavior generally determines the type of control measure to use. Cultural controls often are used to reduce damage to natural stands or plantations of indigenous species,

while direct methods of inoculum removal, either alone or in combination with cultural control methods, may be required to reduce damage in plantations, arboreta, seed orchards, or amenity plantings.

Diseases can be avoided by using the natural balance and diversity of indigenous forests to prevent *Armillaria* epidemics, even though the fungus is present as a minor pest and natural thinning agent. Examples occur worldwide where *Armillaria* causes insignificant damage in indigenous forests but inflicts significant losses when these forests are cleared to establish exotic plantations (see chapters 8 and 9). The cost, both economic and ecological, of converting indigenous forests to exotic plantations must be weighed against any increased commodity value derived from the exotic species.

Needs Assessment

In many situations, *Armillaria* may be present in a forest or orchard and cause little damage. Thus, mere fungal presence is not sufficient cause to treat. Plants that are resistant to *Armillaria* throughout their lives or, as is the case with many conifers, through most of their lives, are capable of maintaining stand or orchard productivity. In such cases, *Armillaria* may act as a thinning agent in young stands (Filip and others 1989, Morrison 1981, Rishbeth 1972a) and as a nutrient recycler in old stands (Durrieu and others 1985, Mason and others 1989, see chapter 8). Disease often is severe in the first few years after plantation establishment, but subsides thereafter. Where this happens, primary inoculum from stumps or other buried woody material is the likely source of disease; secondary inoculum is not effective. Disease in New Zealand's radiata pine plantations (Roth and others 1979), in western North America's young ponderosa pine stands, whether planted or naturally regenerated (Hadfield and others 1986, Hagle and Goheen 1988, Morrison 1981), and in Europe's first-rotation conifer plantations on cleared hardwood sites (Hartig 1873b, Nechleba 1915, Pawsey 1973) follow this pattern.

A high incidence of mortality following establishment may be alarming, but without secondary spread of disease, the economic impact may be insufficient to justify control. Such is generally the case in indigenous ponderosa pine and coastal Douglas-fir stands of western North America (Morrison 1981, Hadfield and others 1986) and in many first-rotation conifers on former hardwood sites in Europe (see chapter 9). In contrast, radiata pine plantations on high-risk sites in New Zealand may lose 50% of the crop within the first 5 years after planting (van der Pas 1981b) which constitutes a severe impact. Direct reductions in primary inoculum (fig. 11.1) may be economically feasible in such



FIGURE 11.1 — Reduction of primary inoculum by removal of stumps and roots of indigenous forest cover in New Zealand prior to establishment of radiata pine plantations. Such actions can markedly reduce disease incidence and severity in first rotation crops (see fig. 9.7). (C. Shaw)

cases; even so, other alternatives also should be considered. For example, increased planting densities that allow for full stocking after suffering losses due to primary inoculum may, if effective, prove more economical and environmentally acceptable than efforts to reduce inoculum levels through stump removal or chemical treatment at the beginning of the rotation. Patchy killing of trees in the plantation may make thinning the remaining stand necessary after mortality has subsided. Contrarily, in orchards and amenity plantings, the economic importance of losing a few or perhaps even a single tree may be sufficient to justify inoculum removal or other costly control procedures. The lack of assessment data in these situations (see chapter 9) complicates decisions to implement control.

As indicated by Rishbeth's survey (1983) of gardens and forests in southern England, the species of *Armillaria* found on a stump, tree, or shrub can affect the decision to initiate control. For example, *A. gallica* had spread widely from an ash stump in a garden with no signs of attacking other trees or shrubs that it had encountered. However, *A. mellea* had spread from a *Prunus* stump and killed species of apple, stonefruit, birch, and sequoia. As identification of *Armillaria* species becomes more routine (see chapters 1 and 2), its use is likely to become standard before control is recommended.

Control Options

Silvicultural Considerations for Natural Forests

In natural forests, silvicultural control of *Armillaria* root disease is frequently an option. Local tree species grown in natural mixtures and densities may resist

Armillaria root disease even though they are known hosts for the local species of *Armillaria*. Where Armillaria root disease is a major concern in coniferous forests in western North America (see chapter 8), only indigenous tree species are grown in production forests. Even so, careful selection among species, seed sources, and cultural methods to match site conditions, particularly those related to habitat type (Daubenmire 1952) or site type (Corns and Annas 1986), is necessary to avoid economic losses. Using locally adapted seed sources for indigenous species that tolerate the disease is recommended for control in the Northwestern United States and Western Canada (Hadfield and others 1986, Morrison 1981, Williams and others 1989).

Substantial losses occurred in mixed coniferous forests of southern Oregon after selective harvest of ponderosa pine overstories (Filip 1977) caused a species composition shift to highly susceptible true firs. Severe root disease problems have been attributed to similar changes in species composition over much of the Western United States due both to selective logging of pines and larch and to fire suppression which favored shade tolerant true firs and Douglas-fir (fig. 11.2, see chapter 8). Dense Douglas-fir and true fir forests are unnatural on these sites and their development often results in disease conditions much like those found in exotic plantations. Current silvicultural practices in such areas, developed in part to reduce root disease losses, aim to re-establish pine, larch, and pine/larch mixtures with

Douglas-fir and true firs composing less than 40% of the regeneration (Hagle and Goheen 1988).

Even when planted within their natural range, some species adapt poorly to certain sites. Although Douglas-fir is well distributed over diverse montane environments, the species has differentiated populations that are closely tied to elevation, latitude, and longitude (Monserud and Rehfeldt 1990, Rehfeldt 1982). Each population has adapted to local environmental conditions and fails to thrive when planted elsewhere. Other conifer species appear to behave similarly (Balmer and Williston 1983, Lotan and Perry 1983, Rehfeldt and others 1984). Thus, attention to seed sources is important for culturing these species. For example, substantial increases in *Armillaria* damage to Scots pine plantations in the German Democratic Republic followed a drought in 1969. Even after the drought, however, wildling pines were seldom affected by the pathogen, leading Kessler and Moser (1974) to recommend development of seed-saving methods to take advantage of natural resistance by regenerating stands through seeding with these sources.

Where use of locally adapted seed sources is not an option because the natural forests were removed, genetic differentiation within artificial populations can be used. Lung-Escarmant and Taris (1989) reported a method to test the *Armillaria* resistance of various pine species in natural stands. They suggested using the

FIGURE 11.2 — A natural forest in western Montana where ponderosa pine is more resistant to *Armillaria* root disease than most associated species. Although few large ponderosa pines remain in the overstory, past management practices that favored removal of ponderosa pine and excluded natural fire have allowed a Douglas-fir and true fir understory to develop that is more susceptible to *Armillaria* root disease. (S. Hagle)



method to test Maritime pine for population, family, and clonal differentiation in resisting *A. ostoyae* within the pine's natural range in southwest France. Whether considering indigenous or exotic trees, genetic differentiation should be matched to the natural site conditions where the trees are growing. Intraspecific variation in adaptation to sites may be great, but the extension of a species' range may still be limited. For example, die-back and declines of silver fir plantations in central and northern Italy are frequently associated with infection by *A. ostoyae*. The diseases appear to be drought-triggered and to be concentrated in fir plantations established in an area "phytologically inferior and warmer" than natural sites for the species (Intini 1989a).

Excessive moisture may have been responsible for the demise of several ponderosa pine plantations which were established during the 1940's in Idaho using non-local seed sources (Hagle unpubl.). The parent trees, growing more than 500 km away, were on very different sites than those where the plantations were established. The plantations were installed to determine if genotypes adapted to dry pine sites would produce superior growth when planted on more mesic, grand fir climax sites. The trees grew exceptionally well for about 40 years but died rapidly thereafter from a combination of pests, among which *Armillaria* root disease was most prominent (Hagle unpubl.). Ponderosa pine has since been found to have "seed zones" of limited range (Squillace and Silen 1962) and planting outside these zones is not recommended. McDonald (1990) discusses how the potential for ecophysiological maladaptation of species to specific sites may influence their susceptibility to *Armillaria* root disease.

Avoiding Hazardous Sites

Matching indigenous species with suitable sites is one way to minimize disease hazard. Sites can be hazardous because they predispose the host in some way, as with off-site plantings. Sites with heavy inoculum loads of pathogenic *Armillaria* species may also be hazardous. Whether a naturally high frequency of *Armillaria* infections occurred in the previous stand or human or other activity increased the level of infection, the influence of inoculum loading is little disputed (see chapter 4). Hazardous sites also may result from site conditions that are unusually favorable to disease development; however, these conditions are difficult to discern because of our limited knowledge of *Armillaria* ecology. Site hazard varies within indigenous forests. For example, soil-related differences in disease severity were reported in Norway spruce stands in central Europe (Gramss 1983). Enhanced survival of stands was usually attributed to the "poor podzolic highland soil

types" to which the spruce appeared to be better suited. The highland soils distinguish low-hazard sites for growing Norway spruce. Ono (1970) found edaphic, topographic, and vegetational relationships with the level of *Armillaria* damage to Japanese larch plantations in Hokkaido, Japan. Williams and Marsden (1982) related root disease patch occurrence in coniferous forests in Montana and Idaho to certain productive soil and habitat types. Byler and others (1990) found that the more productive habitat types in these areas had greater root disease severity than the less productive types, a result that was partially supported in a preliminary report by McDonald and others (1987a).

Damage in exotic plantations or orchards can be minimized by establishing them on sites with a low disease hazard. Sokolov (1964) reported soil types in the Soviet Union influenced the severity of *Armillaria* root disease in mulberry plantations. Severe *Armillaria* root disease in Norway spruce stands in Poland was related to a combination of soil type and elevation (Mańka 1980). The spruce plantations were established on sites previously supporting indigenous stands of silver fir and common beech. Whitney (1984) found *Armillaria* root disease to be more severe on conifers in Ontario, Canada, where soils were coarse-textured and sandy rather than finer-textured and silty.

Vegetation on a site prior to clearing for establishing an orchard or plantation may indicate differences in root disease hazard. For example, Leach (1939) reported site hazard differences for tea plantations associated with indigenous stands of *Muula* trees in eastern Africa. *Muula* roots remain alive but moribund for years after cutting, and these were most often associated with root disease in tea plantations. In Kenya and New Zealand, differences in root disease severity also were noted on lands converted to radiata pine from different indigenous forest types (Gibson 1960, Shaw and Calderon 1977).

Hendrickson (1925) reported *Armillaria* root disease in fruit orchards to be of "widespread economic importance in California." He considered oak roots from the indigenous forest to be the most important source of inoculum, but secondary spread among orchard trees maintained the disease long after the land was cleared of oaks. Cooley (1943) surveyed Eastern U. S. fruit orchards and found little disease except in the sandhill section of North Carolina. Most orchards in this area had been established on land cleared of hardwood forests, indicating that a heavy load of primary inoculum that harbored a pathogenic species of *Armillaria* may have been responsible for the frequency of disease. Orchards themselves may maintain a high hazard from one rotation to the next. For example, *Armillaria* inocu-

lum from a highly susceptible cherry rootstock created hazardous site conditions in replanted orchards of several species in Michigan (Proffer and others 1987).

Vegetation maintained on a site from one crop to the next may affect disease hazard. Although conifer plantations in Britain are damaged by *Armillaria* in the first 10-15 years after planting on sites freshly converted from hardwoods, succeeding rotations of conifers sustain much less damage (Pawsey 1973). Balsam fir Christmas tree plantations are damaged in the first few years after establishment on sites converted from indigenous mixed hardwood and pine forests (Wargo and Houston 1987). Similarly, radiata pine plantations in New Zealand may be severely damaged within 5 years after conversion from indigenous forest but subsequent rotations of pine on the sites may be little damaged (Shaw and Calderon 1977). If this effect is found to be consistent, such areas would be high-hazard sites only for the first rotation after conversion. Recent work in New Zealand, however, suggests that the cursory observations on limited disease incidence in second- or third-rotation pine crops by Shaw and Calderon (1977) may have been premature (MacKenzie and Self 1988).

Resistance

In situ host resistance to root disease is a complex topic as it involves the genetics of both host and pathogen as well as environmental influences. It also can involve managing mixtures of genotypes with varying levels of resistance. Some species with superior resistance or tolerance to infection in one location may be quite susceptible in other locations. For example, Douglas-fir is among the species recommended for planting in Britain where *Armillaria* root disease is especially damaging to Scots pine plantations (Greig and Strouts 1983). It is also considered more resistant than Sitka spruce and grand fir in France (Delatour and Guillaumin 1985). Within its natural range in western North America, however, Douglas-fir is considered rather susceptible to *Armillaria* root disease (Hadfield and others 1986, Hagle and Goheen 1988). In all three locations, *A. ostoyae* is the most common parasite of conifers (Rishbeth 1982, Guillaumin and Lung 1985, Morrison and others 1985a).

Even within limited geographic areas, such discrepancies in resistance can be seen. For example, ponderosa pine's resistance is superior to true firs and Douglas-fir over most of western North America (Morrison 1981, Hadfield and others 1986), but natural ponderosa pine stands in some south-central Washington, sites are severely damaged by *Armillaria* root disease (Shaw and others 1976a, Shaw and Roth 1976). Douglas-fir associated with pine on these sites suffers less damage (Roth and Rolph 1978). A similar situation exists in the Jemez

Mountains of northern New Mexico (Wood 1982, Shaw unpubl.). Thus, intraspecific variation in adaptation to sites may be as great as interspecific variation within the natural ranges of any two or more species.

Radiata pine planted in New Zealand suffers considerable damage from *Armillaria* root disease (Shaw and Calderon 1977), but the same species is not particularly damaged in its natural range in western North America (Raabe 1979a). This variation is probably related to differences in *Armillaria* species, inoculum loads, or edaphic, climatic, or physical site characteristics. Whether endemic or exotic, genetic differentiation in tree species should be compared to site conditions and pathogen species in natural settings in which plants are to be grown, and plantations should be monitored for suitability of the genotypes to the site. Diseases and insect attack are likely to be among the earliest indications of poor compatibility of trees with growing sites.

Relative resistance of many species has been observed in forests, orchards, and parks as well as by controlled inoculation experiments (see chapter 6). Much of this work was completed before many of the pathogenic *Armillaria* species were recognized. As such, the information is only useful in a general way. Morquer and Touvet (1972b) noted considerable variation in resistance of several conifers, but found no species immune to infection by *Armillaria*. Pines were notably susceptible while certain ecotypes of Norway spruce were relatively resistant. Mugala and others (1989) found that white spruce succumbed more readily than lodgepole pine in potted-seedling studies, but these results were inconsistent with field observations where white spruce was damaged less than lodgepole pine (Blenis and others 1987, 1989). In Kenya, Gibson (1960b) noted that slash pine was more severely affected than either radiata or Mexican weeping pine. Rishbeth (1972a) reported that, in a 17-year-old mixed stand of Scots pine and Norway spruce, large patches of pine died while the spruce was virtually unaffected. Day (1927b) observed that, in adjacent 3-year-old plantations of Scots pine and Japanese larch, the pines were more frequently infected than larch but relatively fewer pines were killed. Up to 10% of the larch were killed by *Armillaria*.

Resistant rootstocks have been developed for both fruit and fiber species (Raabe 1966a). Rhoads (1948) reported considerable variation in susceptibility of citrus rootstocks to *Armillaria* and Thomas and others (1948) tested rootstocks of prune and apricot for resistance in California. Armitage and Barnes (1968) reported that loblolly pine resisted *Armillaria*, and a heterospecific graft of slash pine onto loblolly rootstock was sufficiently resistant to replace slash pine killed by the fungus. Peach, almond, apricot, and cherry trees are severely damaged by *A. mellea* in France, while plum is generally resistant

(Guillaumin and others 1989b). The use of resistant rootstocks appears to be the only practicable control option in French stone fruit orchards (Guillaumin and others 1989b). Two rootstocks in particular, resulting from interspecific crosses between diploid plum and peach, appear to satisfy both *Armillaria* resistance and other cultural demands. Heaton and Dullahide (1989b) recommended a number of *Armillaria*-resistant plum, pear, and grape rootstocks for Granitebelt orchards in southern Queensland, Australia.

Perhaps gene manipulation techniques can improve a species' adaptability and physiological resistance to disease, produce populations or clones immune to *Armillaria*, or improve economic qualities of endemic, resistant species (Hubbes 1987). Rootstocks for fruit orchards are prime candidates for receiving resistance genes. Superior quality rootstocks which produce desired growth and compatibility characteristics could be made resistant to *Armillaria* if genes known to produce successful resistance reactions in other species or genotypes can be identified and transferred to the genome of the otherwise superior rootstock. Research to determine the relative resistance of different species and genotypes under a variety of conditions must continue. Additional information is also needed on the nature of resistance (i.e., physiological, genetic, or environmental) and its interaction with various *Armillaria* species and genotypes (see chapter 6).

Using species resistant to *Armillaria* may be economically practicable in some cases, and their suitability may be enhanced by combination with other control procedures. Planting mixtures of species with differing resistance to *Armillaria* may reduce secondary spread of disease in a plantation. For example, Morrison and others (1988) observed fewer and smaller disease patches in plots planted with highly susceptible lodgepole pine or Douglas-fir in alternating rows with resistant western redcedar or paper birch, compared to plots planted only to lodgepole pine or Douglas-fir. Presumably the benefit was derived from limiting secondary disease spread, which limited the size of infection centers.

Other Cultural Considerations

Regeneration methods may influence tree condition and susceptibility to *Armillaria* root disease. For example, Newfoundland conifer plantations that originated from bareroot stock were significantly more damaged by *Armillaria* than those that had been broadcast seeded (Singh and Richardson 1973). Similar results were reported for Scots pine plantations in the German Democratic Republic (Kessler and Moser 1974). Bareroot stock is not always acceptable, however, because of the advantages that accrue from planting (Page 1970, Schubert and others 1970).

Manipulation of rotation length may minimize losses in some situations. As previously mentioned, Norway spruce may be only moderately affected by *Armillaria* root disease. Still, in Czechoslovakian plantations, diameter growth significantly decreased in 70- to 80-year-old spruces (Hřib and others 1983). The current recommendation is to harvest stands by this age, which represents the culmination of mean annual increment. Such pathological rotations are used primarily for economic reasons. They often are an option in hardwood forests in England (Greig and Strouts 1983) and the Eastern United States (Marquis and Johnson 1989), and conifer stands in Ontario, Canada (Whitney 1988b). Stands or individual trees are harvested prior to the age at which they are expected to succumb to *Armillaria* root disease (Marquis and Johnson 1989). A similar principle underlies a recommendation to use training and trellising techniques to promote early cropping in Australian fruit tree orchards where secondary spread of *Armillaria* causes high losses (Heaton and Dullahide 1989b). This practice allows an early recapture of investments and minimizes the economic impact caused by eventual loss of trees to *Armillaria* root disease.

Both precommercial and commercial thinning to reduce damage from *Armillaria* should be considered according to the type of disease caused. Where host condition has little influence over infection and killing by *Armillaria*, thinning is unlikely to reduce losses and may increase damage by providing additional food bases. Precommercial and commercial thinning to reduce intertree competition may effectively reduce disease losses where *Armillaria* is a secondary pathogen, as it is in hardwood forests in southern England and the Eastern United States. Suppressed oaks and pines (completely shaded by overtopping trees) were extensively infected by *A. mellea* and *A. ostoyae* in southern England. Subdominant (codominant) trees in those stands were only slightly infected and apparently resisted extension of infection by these pathogens (Davidson and Rishbeth 1988). Red spruce stands in the Northeastern United States have been severely damaged by *Armillaria* root disease following stagnation from overstocking (Wargo and Shaw 1985). Early thinning has avoided such problems in most managed stands. Precommercial thinning of conifer stands in western North America has produced mixed results (Hagle and Goheen 1988). In one ponderosa pine plantation, mortality rates in thinned and unthinned plots were similar 20 years after precommercial thinning (Filip and others 1989); however, net productivity on the thinned plots increased because of superior volume growth. Singh (1981a) recommended precommercial thinning in pine and spruce stands in eastern Canada to reduce stress and improve resistance to *Armillaria*.

Morrison (1981) advised delaying precommercial thinning in western Canada to 30 years in infection centers of conifer stands where losing residual trees after early thinning could cause low stocking. Blenis and others (1987) observed infections in young lodgepole pine stands in Alberta, Canada, and noted that rhizomorphs spread from the previous stand's debris. They concluded that precommercial thinning could be done after such debris was no longer effective as inoculum.

Interpreting how *Armillaria* root disease responds to commercial thinning or other forms of partial harvest is difficult because stands are often affected by mixtures of two or more root pathogens capable of varying responses. However, in ponderosa pine stands infected with *Armillaria* alone, a partial harvest increased mortality even though the total area affected had remained unchanged (Shaw and others 1976a). Rishbeth (1978b) reported indirect evidence of *A. mellea* spores colonizing oak and ash thinning stumps and thereby causing a low incidence of new infection patches. On this basis, he recommended delayed thinning. Such a delay might, however, lead to even larger and more numerous new infection patches through spore infection of even larger stumps. Severe damage has occurred in New Zealand kiwifruit orchards following spore infection of stumps created by removing windbreak trees (Horner 1988).

Kellas and others (1987) surveyed for *A. luteobubalina* infection in mixed eucalypt stands in Victoria, Australia, where shelterwood cutting has become common. Cutting intensity did not appear to influence the incidence of disease in residual trees and stumps, but frequent, low-intensity cuts may have increased infection. The high infection frequency on residuals in thinned stands also may have reduced growth and increased mortality sufficiently to negate any growth response in the thinned stands.

Partial harvest for commercial thinning or other purposes has caused considerable damage to conifer stands in the Western United States. Byler and others (1986) reported that root disease frequency doubled in stands that had at least one harvest entry compared to those with no tree cutting. Losses to root diseases have been so great following partial harvests which leave stands composed primarily of Douglas-fir or true firs (fig. 11.2) that these silvicultural methods are not recommended on sites prone to root disease in the Western United States (Hadfield and others 1986, Williams and others 1989). Such management activities have truly exacerbated the incidence and severity of *Armillaria* root disease.

Soil pH, organic content, and nutrient status are partially alterable in forestry and orchard operations. Very

little direct evidence, however, establishes the effects of fertilization or other soil amendments on *Armillaria* root disease in forest crops. This may be, in part, because the nutritional requirements of forest species are not well understood. Rykowski (1981a) was not able to decrease mortality rates by applying fertilizers in young Scots pine plantations, but the appearance of chronically infected trees did improve. Fertilization increased the fungistatic effects of extracts from periderm and phloem tissues but also improved the nutritional quality of wood used during the saprophytic phase of *Armillaria* colonization (Rykowski 1983). Application of potassium did, however, significantly reduce damage from *Armillaria* in banana plantations in Malawi (Spurling and Spurling 1975). Use of fertilizers as a management tool in orchards and plantations is further discussed in chapter 9.

Direct Reduction of Inoculum

On the speculation that buried roots and stumps were a source of infection in young orchard trees, Barss (1913) suggested that stumps and roots be removed and that non-orchard species be cropped for several years before establishing an orchard. Since then, recommendations for physical removal of inoculum (Shaw and Roth 1978, 1980) have involved removing diseased trees, uprooting stumps (Roth and others 1980, Arnold 1981), destroying stumps and root remnants (Morrison and others 1988), and turning the earth over to a considerable depth (Heaton and Dullahide 1989b, Horne 1914, McGillivray 1946, Reitsma 1932, Sokolov 1964).

The quantity and location of inoculum that must be removed to prevent disease buildup and spread and the cost of removal justified by the crop's future value are difficult to balance. Complete eradication of the fungus by mechanical, biological, or chemical means is improbable (Williams and others 1989) and of doubtful value. Even sites that have been devoid of woody material for decades, such as land supporting an herbaceous crop, may be re-invaded, albeit slowly, through spore infection when placed into woody plant production (Rishbeth 1978b). Soil disturbance may also stimulate fresh rhizomorph production, increasing the disease risk to newly planted trees (Morrison 1976, Redfern 1970). Excessive removal of woody debris from a site may be detrimental to mycorrhizae as well (Harvey and others 1981, Maser and others 1984). Such additional risk must, however, be evaluated in context with the large quantities of inoculum removed.

Stump and root removal is commonly practiced in preparing sites for fruit orchards and other high-value crops, whether converting from indigenous forest or removing infected trees from the previous crop. This procedure has long been standard where *Armillaria* is a

recognized threat (Wallace 1935, Thomas and Raphael 1935, Hendrickson 1925). In forests, Sokolov (1964) recommended inoculum removal in the USSR, and Morrison and others (1988) successfully reduced inoculum on an infested site in western Canada. The latter treatment involved pushing the trees, roots and all, from the ground followed by a raking which removed most roots over 1.5 cm in diameter. Douglas-fir, lodgepole pine, western redcedar, and paper birch were planted on treated and untreated sites. After 20 years, mortality of Douglas-fir and lodgepole pine in untreated plots was 5-10 times greater than in treated plots.

Areas within a managed, natural ponderosa pine forest in south-central Washington were so severely damaged by *Armillaria* that they had little likelihood of persisting as a commercial forest unless the disease was controlled (Shaw and others 1976a). Here, recently killed sapling and pole-sized trees, and those positioned where they were likely to be infected (Shaw 1980, Shaw and Roth 1974), were pushed over with a bulldozer (fig. 11.3). This method removed nearly intact root systems. Removing infected pine trees and stumps during thinning in this forest has also effectively reduced disease losses (Roth and others 1977, Roth and Rolph 1978). Special guidelines (fig. 11.4) are used to mark symptomatic trees before pushing them over (Roth and others 1977, 1980). Extraction of stumps up to 50 cm in diameter with a vibratory stump puller has also been successful in this area (Arnold 1981).

In New Zealand, *Armillaria* root disease increased the cost of growing first-rotation radiata pine on sites with a high disease hazard by approximately 40% (Shaw and Calderon 1977). This cost approximates the maxi-



FIGURE 11.3 — Pushing trees over with a bulldozer, rather than cutting them off with a saw, is an effective way to remove root systems and remove inoculum on certain soil types. The technique may also be used to create a "root free" zone which may serve as a barrier to further disease spread (see fig. 11.4). (C. Shaw)

mum amount available for disease control. Initial stump uprooting and removal trials (fig. 11.1) suggested that the high disease losses encountered on nontreated sites could be reduced at a cost that was within the calculated economic limits (Shaw and Calderon 1977, Shaw unpubl., van der Pas 1981b). Utilizing stumps and roots may partially offset removal costs (Arnold 1981, Hakkila 1974). In addition, stump removal and plowing can benefit general seedling performance (Department of Forestry Queensland 1972, Morrison and others 1988, Roth and others 1977, Sorochkin 1972).

The value of plants in urban forests, gardens, and orchards often justifies the much higher treatment costs that are associated with inoculum removal. Recommended site preparation for orchards in the Australian Granitebelt consists of ripping to 35 cm so large roots can be removed, then ripping again to 25 cm to remove roots as fine as 1 cm (0.4-inch) diameter, followed by hand removing remaining roots. Without such rigorous site preparation, *A. luteobubalina* kills up to 50% of the newly planted fruit trees (Heaton and Dullahide 1989b). In New Zealand, soil has been extensively sifted to remove even the smallest infected root pieces (fig. 11.5A) to rehabilitate highly susceptible kiwifruit orchards that have suffered severely from *Armillaria* (Horner 1988). In urban settings, Pawsey (1973) recommended removing stumps and roots to whatever degree is practicable.

Stump and root removal is most effective in the following situations. First, removal works well where the pathogen causes a primary disease from existing inoculum but does not continue to spread from secondary inoculum. Second, if secondary inoculum is important in the disease process, then it occurs in distinct patches (not diffuse in stands) and thus makes careful removal over concentrated areas possible. Third, where secondary inoculum is important but the crop can be managed on a short rotation, such as intensively managed fruit orchards, the pathogen has little time for secondary spread from unremoved inoculum pieces.

Stump removal followed by a brief fallow period may increase the effectiveness of inoculum reduction where secondary inoculum is of concern. The presumably small, residual roots would likely decay quickly—particularly in tropical regions. Pits dug for removing infected coffee roots in Kenya either are left open for several months or are treated with a soil sterilant before covering. Still, a short fallow of 3-4 months after treatment is recommended (Baker 1972). Extended fallow periods without stump removal might also prove effective in temperate regions although costly in terms of lost production time (Roth and others 1977).

Rishbeth (1972b) showed that hardwood stumps cut 40

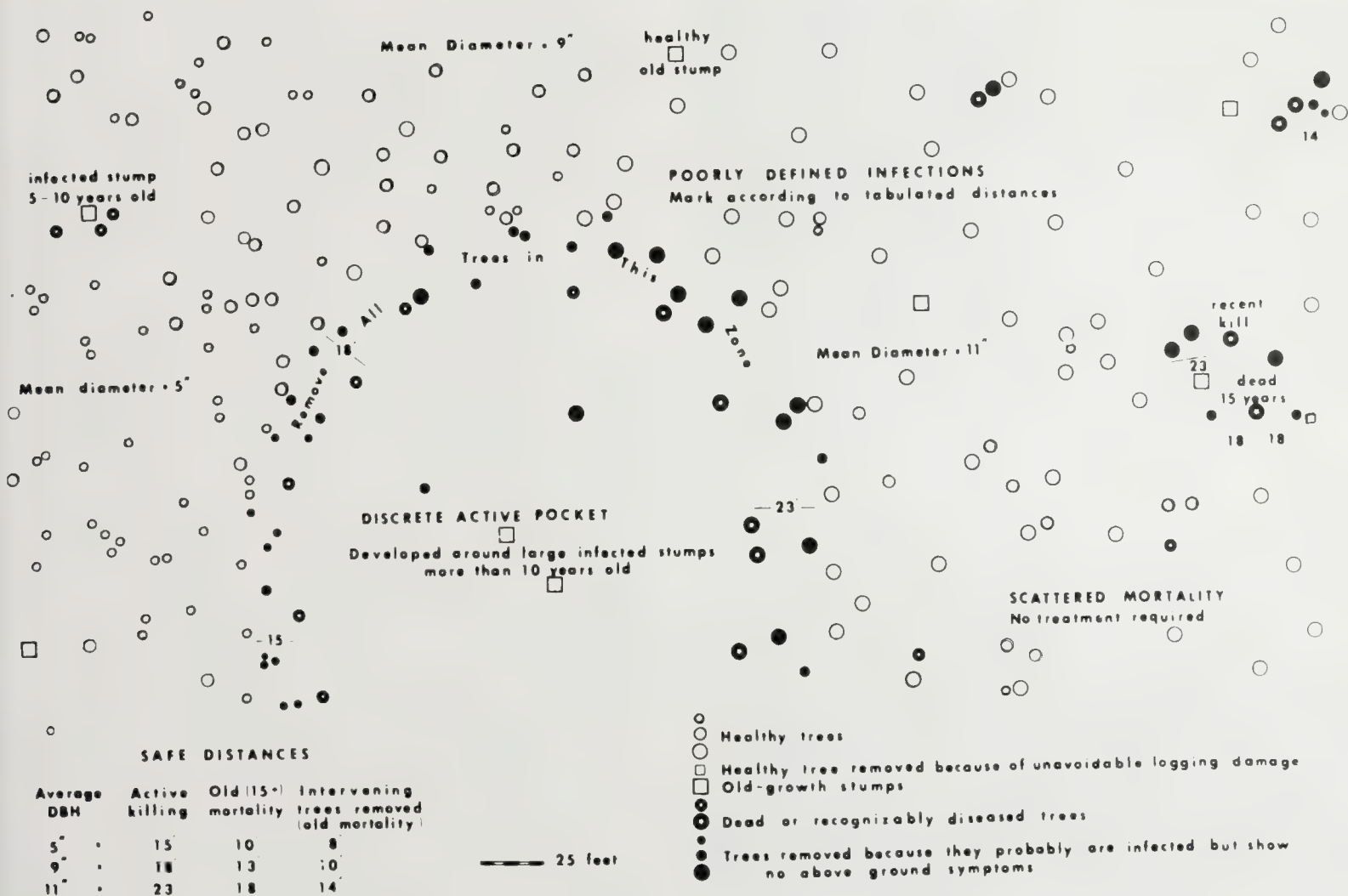


FIGURE 11.4 — Guidelines developed by Roth and others (1977) to treat *Armillaria* root disease in ponderosa pine in south-central Washington. Trees at the left of the *Armillaria* center are too small for commercial thinning and are not disturbed except for removals to establish a barrier at the limits

of the disease pockets. This action is done in conjunction with treatment of the commercial stand at the right by pushing trees over to remove their root systems (see fig. 11.3). (L.F. Roth, *Journal of Forestry*)

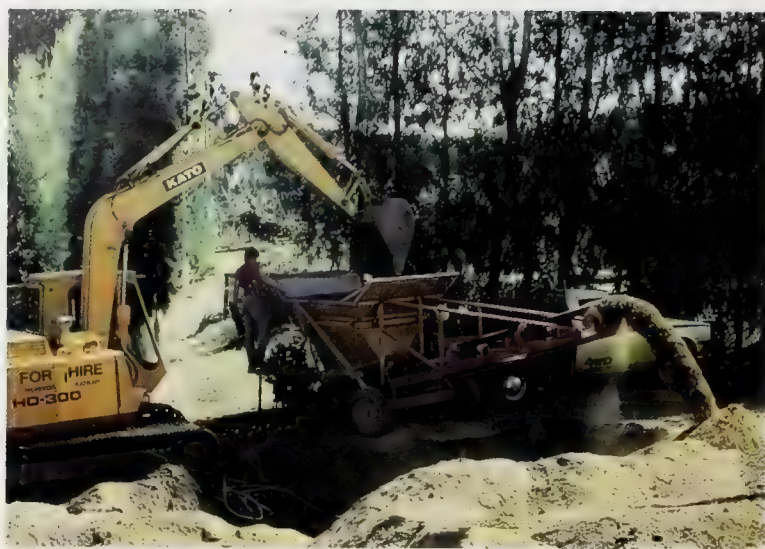
years earlier produced rhizomorphs, but at much lower levels than from younger stumps. The disease is rarely troublesome in first-rotation forests established on natural grassland and former agricultural land. However, the economics of extending the rotation by delaying establishment may prohibit leaving land unstocked for lengthy periods—unless the land can otherwise be profitably used (e.g., livestock grazing or herbaceous cropping) in the interval. Annual cropping with cereals or alfalfa 4-5 years following clearing of orchard sites may deplete most of the nutritional sources for *Armillaria* (Guillamin 1977, Mallet and others 1985) while providing income.

Simply avoiding old planting sites when replanting sections of orchards killed by *Armillaria* is advised for many crops (Horner 1990, Baker 1972, Heaton and Dullahide 1989b). This, combined with stump and root removal, provides an effect similar to fallow before root closure occurs. Heaton and Dullahide (1989b) rec-

ommended avoiding specific locations from which infected trees have recently been removed in orchards by relocating new orchard rows midway between the former rows.

Trenching at least 1.1 m deep to isolate infected plants from healthy parts of a vineyard or fruit orchard is used in France to control spread of *Armillaria* root disease (Guillamin 1977). Trenching 0.6 m (20 inches) in cocoa plantations (Rishbeth 1980) and 1.1 m (3.5 feet) deep in coffee plantations (Wallace 1935) has been used successfully in Africa. Laying a plastic barrier in a trench and then backfilling it with removed soil has also been used for disease control in kiwifruit orchards in New Zealand (fig. 11.5B).

Pruning and girdling diseased roots (Kendall 1931), or drying and aerating the root collar (Munnecke and others 1976, Kendall 1931), may be useful on individual, high-value trees in orchards, parks, gardens, forest



A



B

FIGURE 11.5 — Control of *Armillaria* root disease in kiwifruit orchards in New Zealand (see fig. 9.6). A: Sifting of soil to remove even small pieces of infected roots to rehabilitate a severely diseased orchard. This method is no longer cost effective due to a reduction in kiwifruit profitability. (I.J. Horner) B: If properly placed, trenches lined with plastic and backfilled serve as a mechanical barrier to root and rhizomorph growth into yet-unaffected portions of the orchard. (R.A. Hill)

campsites, and seed orchards (Shaw and Roth 1978, 1980). Levitt (1947) used a water jet to expose root collars of infected citrus trees. Rackham and others (1966) found that exposing root collars effectively controlled *Armillaria* in citrus orchards, but they also noted

that the large craters formed by this control method over a number of years could pose a hazard to workers in the orchards. Sokolov (1964) reported control of *Armillaria* in young Siberian larch by exposing the root collar. Generally, these procedures would be inappropriate in commercial forests because of prohibitive costs.

Chemical Protectants, Eradicants, and Curatives

Apart from soil fumigation with carbon disulphide, methyl bromide, or chloropicrin after removing woody debris, very little experimental evidence supports the effectiveness of the most commonly advocated chemical treatments (Shaw and Roth 1978). Justification for using many of these treatments is based on superficial and subjective criteria (Pawsey and Rahman 1976a). Reviews of chemical control of *Armillaria* have been presented by Pawsey and Rahman (1976a), Shaw and Roth (1978, 1980), and Thies and Russell (1984). As emphasized by Shaw and Roth (1978, 1980), managers must understand whether chemical applications are intended to protect uninfected plants, eradicate the fungus in infected stumps and roots, or treat or cure infected, living plants.

Chemical soil fumigants that destroy *Armillaria* in root fragments are especially useful in orchard, vineyard, and floriculture operations where agricultural methods are applicable (Kissler and others 1973). Methyl bromide, a chemical demonstrated useful for this purpose in 1935 (Richardson and Johnson 1935), is still the most extensively used fumigant because of its non-specific action and good penetrability in soil (Vanachter 1979). Activity of chloropicrin against *Armillaria* in prune root sections was demonstrated in 1936 (Godfrey 1936). It is still a much-used fumigant because it will destroy even the most resistant soil pathogens, although penetration in soil is difficult to achieve. Fruit crops in California have benefited from using carbon disulphide injected at regular intervals over an infected site after removing stumps (Bliss 1951). Heaton and Dullahide (1989b) also recommended using methyl bromide fumigation in orchards by injection into root-free soil and sealing with plastic.

Systemic fungicides which have effectively suppressed *A. ostoyae*, *A. mellea*, and *A. gallica* in vitro are hexaconazole, flutriafol, and fenpropidin (Turner and Fox 1988). Chemicals of the ergosterol biosynthesis inhibitor type are promising candidates for protectants and curatives (Schwabe and others 1984). In fact, systemic fungicides, "which can act both directly on the fungus in the soil and within the plants at some distance from the point of application, have raised great hopes for the control of soil-borne fungal diseases"

(Louvvet 1979). However, as Louvvet (1979) also points out, substantial problems need to be solved before application of systemic chemicals is successful. First, translocating systemics in plants is acropetal whereas basipetal translocation would be more useful in treating roots. Second, strains of pathogens resistant to their action may rapidly appear in crops although evidence for such action in *Armillaria* is currently lacking.

Armillatox, a phenolic emulsion containing 48% active ingredients (unidentified), has been marketed for specific use against *Armillaria*. Apparently, the compound was developed after successfully controlling *Armillaria* with creosote (Bray 1970). Pawsey (1973), however, considered creosote to be phytotoxic, and of doubtful value. Penetration of the material into the wood is minimal. Armillatox did produce some phytotoxic effects at the recommended dilution, even though rhizomorph production was somewhat reduced (Redfern 1971, Pawsey and Rahman 1976b). There was no evidence of remedial effect of Armillatox on established root infections. Pawsey and Rahman (1974) suggest that repeated, regular use of Armillatox might protect against rhizomorph-initiated infection. Redfern (1971) found no beneficial effect from the chemical.

Maneb (Pawsey and Rahman 1976a) and boric acid (Heško 1971, Pawsey and Rahman 1976a) applied to tree root collars and stumps have successfully reduced some rhizomorph production, although Shaw (unpubl.) abandoned trials with boric acid because of severe phytotoxicity. Rykowski (1974b) suggested that field applications of sodium pentachlorophenate (NaPCP) protected young Scots pine from *Armillaria* infection, helped eradicate the fungus in infected stump roots, and did not injure the tree. However, Shaw and others (1980) found NaPCP did not reduce infection on radiata pine inoculated with *Armillaria*, but they did notice some decreases in host vigor. The long-term benefit of such treatments has yet to be demonstrated, and considerable doubt remains about the phytotoxic effects of both boric acid and NaPCP (Shaw and Roth 1978), and about NaPCP's potential effects on human health (Shaw and others 1980).

Filip and Roth (1987) applied chemical to the root collars of small-diameter ponderosa pines to prevent mortality caused by *A. ostoyae* in south-central Washington. After 10 years, none of the seven chemicals (benomyl, captan, copper sulfate, iron sulfate, copper wire, vorlex, or chloropicrin) appeared to reduce mortality. Although single applications of the chemicals to protect pines from lethal infections were not effective, some of the chemicals may protect pines in high-value areas, such as seed orchards, recreation sites, or ornamental plantings, where economics may justify repeated applications.

Fedorov and Bobko (1989) tested several fungicides for controlling existing infections in live hosts by applying them to the rhizosphere. They reduced rhizomorph production using cuprozan, fundazol, derozal, topsin-M, and copper oxychloride, but doubted the overall benefit of the treatments because *Armillaria* remained alive in host tissues. Recently, treating stone fruit trees in Australian orchards with potassium phosphite (fig. 11.6) has shown promising results; 75% of the treated trees appear to be recovering from *Armillaria* infection (Heaton and Dullahide 1989a).

In many chemical tests, effects on rhizomorph production have been the main criterion for effective treatment. However, Redfern (1975) reported a significant negative correlation between the percentage of trees killed by *Armillaria* isolates and dry weight of rhizomorphs produced by the isolate. Rishbeth (1985a) also reported greater rhizomorph production by weakly parasitic *A. gallica* compared to the more aggressive *A. mellea* and *A. ostoyae*. Conceivably, treatment could alter the stump or rhizosphere environment such that the resident *Armillaria* species change, which may result in a difference in rhizomorph abundance. Considering our current understanding of rhizomorph production among different species in situ, this criterion for evaluating treatment effectiveness should be reconsidered (see chapter 4).

Filip and Roth (1977) successfully controlled *Armillaria* in ponderosa pine stumps using methyl bromide, Vorlex, chloropicrin, carbon disulphide, and Vapam (fig. 11.7). Chloropicrin, Vortex, and methyl bromide eliminated the fungus from the stumps. In high-value crops and ornamentals where stump removal may not



FIGURE 11.6 — Injection of a peach tree with potassium phosphite as treatment for prior infection by *Armillaria* root disease. Development of epicormic branches along the stem indicates success. Infected trees can apparently recover following such treatments, but resumption of full production remains to be shown. (J.B. Heaton)



A



B



C

FIGURE 11.7 — Chemical treatment of ponderosa pine stumps to eradicate *Armillaria*. Holes are drilled in stumps (A) as entry ports for liquid eradicator chemicals (B) or gaseous fumigants

(C). Many such treatments successfully eliminated *Armillaria*, but costs were considered too high for general applications in forestry. (Filip 1976, Filip and Roth 1977). (G. Filip)

be desirable or possible (such as where access with heavy machinery needed for removal is limited), fumigants may be a useful option. Fumigant injections to establish barriers which prevent vegetative spread of *Armillaria* may also be valuable (Houston 1975, Filip and Roth 1977) in forestry applications.

The significant economic losses caused by *Armillaria* justify further efforts in chemical control (Pawsey and Rahman 1976a). In certain situations, chemical treatments may alter disease development at the epiphytotic level (Filip and Roth 1977). However, certain aspects of such work need to be stressed. For example, field studies must define treatments by specific objectives—i.e., protecting, eradicating, or curing. Disease condition prior to treatment (i.e., proportion of stump colonized) must be known. Techniques for assessing effectiveness must be both valid and definitive. The cost/benefit of treatment must be evaluated in context with alternative measures and crop value. Detrimental effects of the treatment on the environment or society require consideration. One potential advantage for chemical protectants is that the critical region for application is likely to be the root collar, thus limiting the area requiring treatment. For seedlings, a protectant chemical should be relatively inexpensive, safe, easy to use, easy to apply at planting, nonphytotoxic, nonpersistent, or fungistatic, and persistent in the region of

application. As discussed below, the control achieved by some chemicals may be interrelated with their effects on other microorganisms.

Biological Control and its Integration with Other Methods

Biological control of a plant pathogen has several inherent advantages (Hunt and others 1971). Among others, it is more likely to be accepted by the public than either chemical control or the expense and initial unsightliness of stump and root removal. To control *Armillaria*, a rhizosphere or wood-inhabiting organism might function by inhibiting or preventing rhizomorph and mycelial development, by limiting the pathogen to substrate already occupied, by actively preempting the substrate, or by eliminating *Armillaria* (perhaps through replacement) from substrate already occupied. Pursuing these potential benefits must, however, be tempered with the feasibility of the technique (Shaw and Roth 1978, 1980).

Rishbeth (1976) noted two important features that make control of *Armillaria* by introduced organisms difficult. First, *Armillaria* has a positional advantage over introduced fungi since it already may occupy a portion of the substrate. Second, although *Armillaria* does not colonize wood quickly, it spreads rapidly in

the cambial zone of freshly killed trees. He suggested that antagonistic organisms might not be able to prevent *Armillaria* from becoming established in stumps, but they may restrict further stump colonization and thus limit the available food base. The same logic has been used to suggest that *Armillaria* species of limited pathogenicity may serve as biological control agents for *Heterobasidion annosum* (Fr.) Bref. (Morrison and Johnson 1978; Shaw 1989b,c).

Perhaps the most thoroughly studied antagonists of *Armillaria* are *Trichoderma* species (fig. 11.8) from which two fungitoxic substances, trichodermin and an unidentified compound, have been isolated (Ishikawa and others 1976). Aytoun (1953) studied in vitro interactions of *Trichoderma* and *Armillaria* and concluded that *Trichoderma* must be considered a possible controlling factor in the spread of pathogenic fungi. Sokolov (1964) found fungi in six genera, including *Trichoderma*, *Penicillium*, and *Peniophora*, antagonized *Armillaria*. He recommended using *T. viride* Pers.:Fr. as a control for *Armillaria* root disease. Dubos and others (1978) found that the medium in which *T. viride* inoculum was grown altered the degree to which the antagonist inhibited rhizomorph production by *Armillaria*. Morquer and Touvet (1972a) suggested growing *T. viride* for *Armillaria* control on a "lactoserum" medium.

Trichoderma species are common and ubiquitous soil inhabitants (Aytoun 1953, Griffin 1972), which might suggest that applying *Trichoderma* inoculum is generally unnecessary. *Trichoderma* has been implicated in *Armillaria* control using sublethal doses of fumigants (Bliss 1951, Ohr and others 1973, Filip and Roth 1977),

sublethal heating or drying treatments (Rackham and others 1966, Munnecke and others 1976), and possibly fire (Reaves and others 1990). *Scytalidium lignicola* Pesante also produces a toxin with antifungal properties toward *Armillaria* (Cusson and LaChance 1974). *Armillaria* growth in culture is halted by either *Scytalidium* or its toxin, scytalidin. Since both *Trichoderma* and *Scytalidium* are common in soil, the basis for improving their ability to control *Armillaria* lies in shifting the balance among the fungal populations. An inability to maintain effective populations of organisms antagonistic to *Armillaria* under field conditions has been the main factor limiting successful biological control (Shaw and Roth 1978, 1980).

Bliss (1951) demonstrated the ability of *T. viride* to replace *Armillaria* in artificially infected root segments fumigated with carbon disulphide (CS_2). Garrett (1957, 1958) showed that CS_2 can directly damage *Armillaria* mycelium; pure cultures of *T. viride*, in the absence of fumigation, also killed *Armillaria*. Apparently, both direct fumigant toxicity and subsequent action of *T. viride* were killing *Armillaria* in fumigated soils. After fumigation (fig 11.7C), Filip and Roth (1977) frequently isolated *T. viride* from pine stumps in which *Armillaria* was no longer viable. Munnecke and others (1973) suggested that after fumigation with CS_2 or methyl bromide, a lag period for *Armillaria* growth occurred, indicating a "weakening" of the *Armillaria*. *Trichoderma viride*, being more tolerant of the chemical (Ohr and others 1973), was able to exploit the lag period and exert an antagonistic action on *Armillaria*.

Riffle (1973) noted that two mycophagous nematodes greatly reduced mortality of ponderosa pine seedlings inoculated with *Armillaria*. The nematodes apparently reduced fungal vigor and growth. In vitro studies of how mycophagous nematodes affect mycelia of *Armillaria* and *Trichoderma* species indicated a possible role of *Aphelenchus avenae* in controlling *Armillaria* in a French vineyard. The nematode destroyed the hyphae of *Armillaria* but grew well on *T. polysporum* (Link ex Pers.) Rifai without reducing its growth (Cayrol and others 1978).

Armillaria produces antibiotic compounds (see chapter 3). Oduro and others (1976) suggested that such activity may be an important factor in surviving attack by antagonistic soil microorganisms. Significantly, Ohr and Munnecke (1974) showed that sublethal methyl bromide fumigation prevented the production of antibiotics by *Armillaria*. Munnecke and others (1976) suggested that heating or drying may similarly affect *Armillaria*. The critical factor is that *Armillaria* is stressed. The factors causing the stress may concurrently stimulate antagonistic organisms, resulting in further damage to the already weakened *Armillaria*.



FIGURE 11.8 — Test of antagonism between *A. luteobubalina* and *Trichoderma* sp. Karri wood blocks previously colonized by *A. luteobubalina* (left) and *Trichoderma* sp. (right) were placed face-to-face in soil for 6 weeks, separated and split, and isolations made at 1-cm intervals back from the contacting faces of each block. Green pins indicate recovery of *Trichoderma* sp., red pins *A. luteobubalina*. Penetration of *Trichoderma* sp. into the wood block previously colonized by *A. luteobubalina* was apparently stalled by the zone line. (E. Nelson)

Direct competition for the woody substrate may be an important natural control of *Armillaria*. Garrett (1956b) hypothesized that root-inhabiting parasites would have a low competitive saprophytic ability (see chapter 4). Redfern (1968) suggested that *Armillaria* probably cannot survive indefinitely as a saprophyte and that control is perhaps most easily achieved in the saprophytic phase. Leach (1937) observed that *Rhizoctonia lamellifera* Small prevented *Armillaria* from colonizing tea roots. Sokolov (1964) also observed that spruce stumps colonized by *Lenzites saepiaria* Fr. and *Peniophora gigantea* (Fr.) Massee were not invaded by *Armillaria*. From laboratory tests, Orlos (1957) thought *Fomes pinicola* (Swartz:Fr.) Cke. might be useful in controlling *Armillaria* because of its greater growth rate and ability to exclude *Armillaria* from occupied media. Fedorov and Bobko (1989) tested 10 basidiomycetes which were capable of excluding *Armillaria* from occupied substrates. Two of these, *Peniophora gigantea* (Fr.) Massee and *Pleurotus ostreatus* (Jacq.:Fr.) P. Kumm.,

also effectively prevented *Armillaria* growth in freshly cut stumps into which they had been inoculated.

Coriolus versicolor (L.:Fr.) Quél, *Stereum hirsutum* (Willd.:Fr.) S.F. Gray, and *Xylaria hypoxylon* (L.:Fr.) Grev. inoculated into karri thinning stumps simultaneously with *A. luteobubalina* (fig 11.9) each significantly reduced colonization by *Armillaria* (Pearce and Malajczuk 1990b). The eucalypt stumps were colonized both above and below ground by the competing fungi, but they were more effective antagonists above ground. A naturally occurring, cord-forming species of *Hypholoma* proved to be even more competitive with *Armillaria*, in some cases excluding it entirely.

Such cord-forming, wood-decay fungi have a similar niche to *Armillaria* and are perhaps the most exciting recent discovery in relation to its possible biological control. They are capable of subcortical mycelial growth in stumps and occupy the same initial sites as



RE 11.9 — Successful establishment of antagonistic fungi on karri stumps inoculated with *A. luteobubalina*. Stump inoculated with either *Coriolus versicolor* (A) or a *Hypholoma* significantly reduced colonization by *A. luteobubalina*. Competing fungi colonized the eucalypt stumps both above

B and below ground, but were more effective competitors above ground. A naturally occurring, cord-forming species of *Hypholoma* proved to be even more competitive with *Armillaria*, in some cases excluding it entirely (Pearce and Malajczuk 1990b). (E. Nelson)

Armillaria (Redfern 1968). According to Rayner (1977), cord formers "closely paralleled *A. mellea* in their behavior, except for their lack of pathogenicity." Further studies have indicated that several species of cord-forming basidiomycetes, in particular *Phanerochaete velutina* (DC per Pers.:Fr.) Karst., *Hypholoma fasciculare* (Huds.:Fr.) Kumm., and *Steccherinum fimbriatum* (Pers.:Fr.) J. Erikss., have considerable potential to spread and colonize woody debris in field sites. Several produce networks of mycelial cords in soil and litter (Dowson and others 1988a) which can infest additional woody substrates (Dowson and others 1988b). Populations of some cord formers can be manipulated by chemically treating stumps (Rayner 1977), a finding that indicates potential to artificially induce biological control of *Armillaria*. Ammonium sulphamate appears particularly useful as it increased colonization and decay by cord-formers of below-ground portions of treated beech and birch stumps (Rayner 1977).

Stump fumigation has excluded or eradicated *Armillaria* directly in lethal doses (Bliss 1951, Rackham and others 1966, Filip and Roth 1977). Sublethal doses, however, do not kill *Armillaria* directly, but allow competing fungi less affected by the chemical to replace it. (Munnecke and others 1973, Ohr and others 1973). Sublethal doses of methyl bromide injected into orchard soil in California successfully controlled *Armillaria* (Munnecke and others 1981). *Trichoderma* spp., which resisted the methyl bromide, may have been responsible for controlling *Armillaria* in the fumigated soil. Formaldehyde was used in sublethal doses to control *Armillaria* in apple and pear orchards in China (Chang and others 1983), where *Trichoderma* populations were stimulated by the treatment and were credited with the control.

Silvicides which can rapidly kill host tissues are used to kill trees before cutting in tropical regions where the killed roots decay rapidly and pathogens are readily replaced by saprophytes (Mallet and others 1985). However, in temperate regions, the rapid killing by herbicides may benefit *Armillaria*. For example, Rishbeth (1976) reported that stump treatment with 2,4,5-T favored *Armillaria* colonization; and Pronos and Patton (1979) found more rhizomorph production 10 years after treatment in stumps of herbicide-killed oaks than in girdled oaks. Rapid death from the herbicide treatment was thought to have favored *Armillaria* over competing saprophytes.

While stump colonization is an important factor in *Armillaria* root disease, the nutritional quality of stumps and roots will influence the longevity of the pathogen. Leach's report (1937) that ring-barking effectively controlled the spread of *Armillaria* in African tea plantations led to several investigations into the nutri-

tional suitability of altered stumps for *Armillaria*. Leach (1939) suggested that decreased concentrations of stored carbohydrates within the roots of ring-barked trees rendered them unsuitable for *Armillaria* colonization. Ring-barking also could have rendered the roots more easily colonized by other, saprophytic fungi and thus quickly reduced the volume of material available for *Armillaria*.

Redfern (1968) found that ring-barking or poisoning mature oaks 1 year prior to felling in Britain resulted in more rapid decay of the roots by *Armillaria* compared to those felled without prior treatment. Rhizomorph production may have been a major influence in Redfern's study. While rhizomorphs may be scarce in African soils (Wiehe 1952), they are abundant and proliferate epiphytically on live tree roots in Britain where localized lesions on live roots are also common. Ring-barking and silvicide treatment favored the invasion of the already present parasite. The roots of the treated oaks either initially were not a good substrate, or deteriorated quickly because significantly fewer rhizomorphs were produced from sections of treated roots compared to roots of non-treated trees 5 years after felling. Neither ring-barking nor silvicide treatment was effective in reducing mortality in subsequent plantations.

Lanier (1971) indicated that girdling old Scots pine and common beech a year before felling reduced the number of young pines attacked. Disease incidence was low, however, even in untreated parts of the forest. Punter (1963) indicated that girdling reduced neither the mortality of young trees nor the number of *Armillaria* basidiomes on stumps. Swift (1970) concluded that ring-barking effectively prevented invasion of stumps from external inoculum sources, but spread of the fungus from pre-existing lesions was not inhibited and probably was enhanced.

Heating and drying methods such as those employed by Birmingham and Stokes (1921) and Rackham and others (1966) are costly, difficult to apply, and almost certainly limited in utility to orchard and ornamental situations. Broadcast burning after clearfelling of indigenous forest in New Zealand significantly reduced the number of viable rhizomorphs compared to counts before clearfelling (Hood and Sandberg 1989). However, all the pine plantations described in New Zealand as having suffered severe losses from *Armillaria* (Shaw and Calderon 1977) were on sites burned during preparation for planting. Apparently, such reductions in rhizomorphs are not sufficient to control the disease. Focan and others (1950) noticed that root disease increased among perennial plants established after burning, and *Trichoderma* spp. markedly declined. However, Reaves and others (1990) reported that recovery of

Trichoderma isolates from soil was unaffected by fire. The species composition shifted such that, after burning, the most frequently isolated species had a greater antagonism towards *Armillaria*.

Mycorrhizae have been suggested as a protection against parasitic attack by *Armillaria*. Gaudray (1973) postulated that the formation of mycorrhizae on exotic Sitka spruce in France is incomplete and thus affords inadequate protection against *Armillaria*. Studies in vitro have shown that mycorrhizal fungi can inhibit *Armillaria* (Eghbaltalab and others 1975). Direct protection by mycorrhizae seems unlikely, however, as the main infection sites for *Armillaria* are on coarse roots rather than the fine roots where mycorrhizae develop.

Examining natural populations of organisms that are antagonistic to the identified, parasitic species of *Armillaria* present on sites that express different severities of root disease may be useful. Such examinations may indicate characteristics that could be manipulated through management so as to favor antagonistic organisms.

Conclusions

Whether to invest in *Armillaria* control and selecting control methods are decisions that need to be based on the value of losses in the absence of control. Assessing impact to commodity production or other features such as amenity value may, in itself, be costly, but it is an important precursor to any control decision. Both monetary and environmental costs of various control alternatives should be justified by commodity or other values derived. Effectiveness of control in a particular situation is another important consideration. For example, stump removal that reduces inoculum by 60% may greatly improve the productivity of a crop for which primary inoculum is the major concern, or of a crop that is produced in a short time. But stump removal with this same level of inoculum reduction may only slightly improve the productivity of a crop subject to secondary disease spread.

Control projects must be monitored long-term in most crops to measure relative gains from treatment (Jančařík 1955). Fruit orchards that are subject to secondary spread of *Armillaria* may require monitoring over decades to evaluate treatment fully. Forests may require a century or more to reach maturity. If disease spread from secondary inoculum is of concern, then monitoring for at least 20-30 years may be required to assess control effectiveness. How the effectiveness may carry over into subsequent rotations also needs to be considered because little information is available on

this subject (see chapter 10). In such cases, interim evaluation and some degree of faith in projections are necessary.

In summary, the following checklist needs to be considered before any attempts are made to control *Armillaria* root disease.

- (1) Critically evaluate disease impact to ensure that the level of loss justifies control. The use of disease models may aid this effort (see chapter 10).
- (2) Control through cultural modifications should be given first priority, particularly in forests. As our current forest management rarely emulates nature's processes, pathologists must work in direct cooperation with foresters to understand and modify disease-stimulating practices.
- (3) Utilize resistant or tolerant species, genotypes, or rootstocks, if known, that are compatible with other necessary values. Ensure that the host genotype selected for resistance is suitable for planting on potential sites, and will provide for the planned end use of the fruit or fiber. Pursue opportunities to genetically engineer *Armillaria*-resistant or tolerant species.
- (4) When establishing new plantations or orchards, exercise care in site selection. Small-scale trials to evaluate disease potential should be established prior to large-scale land clearing and plantation or orchard development. If the site is found to have a high disease hazard, then one must be prepared for costly preestablishment actions such as inoculum removals by more thorough site preparation, postponement of plantation or orchard establishment for some unknown period, or elimination of the site from further consideration.
- (5) Maintain the general health of the forest, orchard, or amenity planting by preventing damage from other agents, avoiding adverse sites, and discouraging detrimental human activities.
- (6) Direct reductions of inoculum levels by physical removal of stumps and roots requires careful economic and ecological analysis. The effectiveness of such treatments in orchards, exotic plantations, and amenity plantings is generally appreciated; their effectiveness in natural forests will be better understood within the next few years when results from existing, long-term trials become available.
- (7) When considering chemical treatments, clearly differentiate among protectants, eradicants, and

curatives. Except for high-value fruit or amenity trees, curatives are likely to be uneconomical. Even in orchards and amenity plantings, chemical applications need to be realistically evaluated for their relative cost/benefit. For chemical treatment of stumps, consider compounds that can be translocated, particularly basipetally. Protectants should be inexpensive, easy to handle and apply, nonphytotoxic, fungitoxic or fungistatic, and relatively persistent. Possible environmental and human health hazards require consideration.

(8) Fumigation, girdling, and silvicide treatment before felling may be useful methods to employ in preparing land for orchards, ornamentals, and some forestry applications such as seed orchards and test plantations. Fallowing after such treatment may improve effectiveness, especially where disease spread from secondary inoculum is anticipated.

(9) Biological control is desirable but requires further development for practical application in most

situations. Research on antagonists, particularly cord-formers, needs to continue as does work on the various actions (i.e., fire, chemicals) that might be used to alter conditions in a way that favors developing and maintaining populations of desirable, antagonistic organisms.

Armillaria control needs to be a thoughtful, reasoned process, not a random or haphazard one. Evaluating the necessity for control and, if found necessary, determining the best option to implement are integral to prudent stewardship of forests, orchards, and amenity plantings. Our increased understanding of species identity, their pathogenic behaviors, and ecological relationships offers the opportunity for a systematic evaluation of approaches to controlling *Armillaria* root disease. Combined with results from long-term tests of inoculum removal and evidence of some new developments in genetic resistance, chemical effectiveness, and biological methods, success should be greater in the future than it has been in the past.

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Scientific and Common Names of Plants Noted in This Book

Common Names — Scientific Names

COMMON NAMES	SCIENTIFIC NAMES
acacia	<i>Acacia</i>
African oilpalm	<i>Elaeis guineensis</i>
Agathis	<i>Agathis</i>
ailanthus	<i>Ailanthus</i>
albizia	<i>Albizzia falcata</i> Merr.
albizia	<i>Albizzia</i>
alder	<i>Alnus</i>
almond	<i>Prunus amygdalus</i> Batsch.
alpine ash	<i>Eucalyptus delegatensis</i> R.T. Bak.
American chestnut	<i>Castanea dentata</i> (Marsh.) Borkh.
American beech	<i>Fagus grandifolia</i> Ehrh.
apple, pome fruit	<i>Malus</i>
apricot	<i>Prunus armeniaca</i> L.
araucaria	<i>Araucaria</i>
Arizona pine	<i>Pinus arizonica</i> Engelm.
Arizona pine	<i>Pinus ponderosa</i> var. <i>arizonica</i> (Engelm.) Shaw
ash	<i>Fraxinus</i>
avocado	<i>Persea</i>
Bahaman pine	<i>Pinus caribaea</i> var. <i>bahamensis</i> Barr. ex Golf.
balsam poplar	<i>Populus balsamifera</i> L.
balsam fir	<i>Abies balsamea</i> (L.) Miller
banana	<i>Musa</i>
banksia	<i>Banksia</i>
barkclothtree	<i>Brachystegia</i>
beech	<i>Fagus</i>
beefwood	<i>Casuarina</i>
beet	<i>Beta</i>
bigtooth aspen	<i>Populus grandidentata</i> Michx.
birch	<i>Betula</i>
black currant	<i>Ribes nigrum</i> L.
black oak	<i>Quercus velutina</i> Lamarck
black spruce	<i>Picea mariana</i> (Mill.) B.S.P.
blackberry, raspberry	<i>Rubus</i>
broad-leaved peppermint	<i>Eucalyptus dives</i> Schau.
broom	<i>Cytisus</i>

COMMON NAMES

brown barrel
brown salwood
cacao
cactus
cane
Caribbean pine
carrot
cassava
ceanothus
cedar
cedrela
chaulmoogratree
cherry
chestnut
chocolatetree
cinchona
citrus
cocoa
coconut
coffee
colanut
common ash
common fig
common teak
common chaulmoogratree
common beech
common pistachio
common pomegranite
common tea
cork oak
Corsican pine
cotton
cryptomeria
currant, gooseberry
cypress
cypress pine
cypress pine
dacrydium

SCIENTIFIC NAMES

<i>Eucalyptus fastigata</i> Deane & Maid.
<i>Acacia mangium</i> Willd.
<i>Theobroma cacao</i> L.
<i>Opuntia</i>
<i>Arundinaria</i>
<i>Pinus caribaea</i> Morelet
<i>Daucus</i>
<i>Manihot</i>
<i>Ceanothus</i>
<i>Cedrus</i>
<i>Cedrela</i>
<i>Hydnocarpus</i>
<i>Prunus</i>
<i>Castanea</i>
<i>Theobroma</i>
<i>Cinchona</i>
<i>Citrus</i>
<i>Theobroma</i>
<i>Cocos</i>
<i>Coffea</i>
<i>Cola</i>
<i>Fraxinus excelsior</i> L.
<i>Ficus carica</i> L.
<i>Tectona grandis</i> L. f.
<i>Hydnocarpus anthelminticus</i> Pierre
<i>Fagus sylvatica</i> L.
<i>Pistacia vers</i> L.
<i>Punica granatum</i> L.
<i>Camellia sinensis</i> (L.) Ktze.
<i>Quercus suber</i> L.
<i>Pinus nigra</i> var. <i>maritima</i> (Ait.) Melville
<i>Gossypium</i>
<i>Cryptomeria</i>
<i>Ribes</i>
<i>Cupressus</i>
<i>Widdringtonia</i>
<i>Callitris</i>
<i>Dacrydium</i>

COMMON NAMES	SCIENTIFIC NAMES	COMMON NAMES	SCIENTIFIC NAMES
dawn redwood	<i>Metasequoia</i>	Japanese larch	<i>Larix leptolepis</i> (Sieb. & Zucc.) Gord.
deodar	<i>Cedrus deodora</i> G. Don ex Loud.	jarrah	<i>Eucalyptus marginata</i> Donn ex Smith
Douglas-fir	<i>Pseudotsuga menziesii</i> (Mirb.) Franco	jujube	<i>Zizyphus</i>
Douglas-fir	<i>Pseudotsuga</i>	karri	<i>Eucalyptus diversicolor</i> F. Muell.
downy oak	<i>Quercus pubescens</i> Willd.	kauri	<i>Agathis australis</i> Salisb.
eastern white pine	<i>Pinus strobus</i> L.	Khasi pine	<i>Pinus kesiva</i> Boyle ex Gordon (<i>P. insularis</i> Endl.)
eastern hemlock	<i>Tsuga canadensis</i> (L.) Carr.	khaya	<i>Khaya</i>
elm	<i>Ulmus</i>	kiwifruit	<i>Actinidia</i>
Engelmann spruce	<i>Picea engelmanni</i> Parry ex Engelm.	Korean pine	<i>Pinus koraiensis</i> Sieb. & Zucc.
English oak	<i>Quercus robur</i> L. (<i>Q. pendunculata</i> Ehrh).	larch	<i>Larix</i>
eucalypt-gum	<i>Eucalyptus</i>	lavender	<i>Lavandula</i>
European larch	<i>Larix decidua</i> Mill.	leadtree	<i>Leucaena</i>
falsecypress	<i>Chamaecyparis</i>	lime	<i>Citrus aurantifolia</i> (Christmann in L.) Swingle
fig	<i>Ficus</i>	litchi	<i>Litchi</i>
fir, true fir	<i>Abies</i>	loblolly pine	<i>Pinus taeda</i> L.
fish pelargonium	<i>Pelargonium hortorum</i> Bailey	locust	<i>Robinia</i>
flooded gum	<i>Eucalyptus grandis</i> Hill ex Maid.	lodgepole pine	<i>Pinus contorta</i> Dougl. ex Loud.
geranium	<i>Pelargonium</i>	loganberry	<i>Rubus loganobaccus</i> L. Bailey
gliricidia	<i>Gliricidia</i>	loquat	<i>Libotrya</i>
gmelina	<i>Gmelina</i>	macadamia	<i>Macadamia</i>
gmelina	<i>Gmelina arborea</i> L.	Mahaleb cherry	<i>Prunus mahaleb</i> L.
gooseberry, current	<i>Ribes</i>	mahogany	<i>Swietenia</i>
granadilla	<i>Passiflora</i>	mango	<i>Mangifera</i>
grand fir	<i>Abies grandis</i> (Dougl. ex D. Don) Lindl.	maple	<i>Acer</i>
grape	<i>Vitis</i>	Maritime pine	<i>Pinus pinaster</i> Ait.
greatcone banksia	<i>Banksia grandis</i> Willd.	messmate stringybark	<i>Eucalyptus obliqua</i> L'Hérit.
green wattle	<i>Acacia decurrens</i> (Wendl.) Willd.	Mexican weeping pine	<i>Pinus patula</i> Schiede & Deppe
grevillea	<i>Grevillea</i>	Mexican cypress	<i>Cupressus lusitanica</i> Mill.
guava	<i>Psidium</i>	mlanji cedar	<i>Widdringtonia whytei</i> Rendle
Hankow willow	<i>Salix matsudana</i> Koidz.	Morinda spruce	<i>Picea morinda</i> Link
hazelnut	<i>Corylus</i>	mountain pine	<i>Pinus uncinata</i> Mill. ex Mirb.
hemlock	<i>Tsuga</i>	mountain ash	<i>Eucalyptus regnans</i> F. Muell.
hickory	<i>Carya</i>	mountain gray gum	<i>Eucalyptus cypellocarpa</i> L. Johnson
hinoki	<i>Chamaecyparis obtusa</i> Endl.	mountain hemlock	<i>Tsuga mertensiana</i> (Bong.) Carr.
Honduran pine	<i>Pinus caribaea</i> var. <i>hondurensis</i> Barr. & Golf.	mulberry	<i>Morus</i>
Honduras mahogany	<i>Swietenia macrophylla</i> King	Muula	<i>Parinari mobola</i> F. Muell. ex Benth.
hops	<i>Humulus</i>	myrtle-beech	<i>Nothofagus cunninghamii</i> (Hook. f.) Oerst.
Hungarian oak	<i>Quercus frainetto</i> Ten.	narrow-leaved	<i>Eucalyptus radiata</i> Sieb. ex DC
incense-cedar	<i>Calocedrus decurrens</i> (Torr.) Florin (<i>Libocedrus decurrens</i> Torr.)	peppermint	<i>Eucalyptus deglupta</i> Blume
incense-cedar	<i>Calocedrus</i>	New Guinea gum	<i>Solanum</i>
Indian fig	<i>Opuntia ficus-indica</i> Mill.	nightshade	
Indian pipe	<i>Monotropa hypopitys</i> L.	northern California	
Indian pipe	<i>Monotropa</i>	walnut	<i>Juglans hindsii</i> Jeps. ex Smith
Indian pipe	<i>Monotropa uniflora</i> L.	Norway spruce	<i>Picea abies</i> (L.) Karst.
iron tree	<i>Metrosideros</i>	oak	<i>Quercus</i>
jack pine	<i>Pinus banksiana</i> Lamb.	ohia	<i>Metrosideros polymorpha</i> (Gaug.) Rock
Japanese redcedar	<i>Cryptomeria japonica</i> (L.) D. Don		

COMMON NAMES	SCIENTIFIC NAMES	COMMON NAMES	SCIENTIFIC NAMES
oilpalm	<i>Elaeis</i>	silver maple	<i>Acer saccharinum</i> L.
olive	<i>Olea</i>	silver wattle	<i>Acacia dealbata</i> Link
orchid	<i>Gastrodia cunninghamii</i> Hook. f.	Sitka spruce	<i>Picea sitchensis</i> (Bong.) Carr.
orchid	<i>Gastrodia elata</i> Bl.	slash pine	<i>Pinus elliotii</i> Engelm.
orchid	<i>Gastrodia</i>	snowbrush	<i>Ceanothus velutinus</i> Dougl.
orchid	<i>Galeola</i>	sour cherry	<i>Prunus cerasus</i> L.
orchid	<i>Galeola septentrionalis</i> Reichb. f.	sour orange	<i>Citrus aurantium</i> L.
papaya	<i>Carica</i>	southern blue gum	<i>Eucalyptus globulus</i> Labill. ssp. <i>bicostata</i> (Maid et al.) Kirkp.
paper birch	<i>Betula papyrifera</i> Marsh.	southern-beech	<i>Nothofagus</i>
paraserianthes	<i>Paraserianthes</i>	spike barkclothtree	<i>Brachystegia spiciformis</i> Benth.
paraserianthes	<i>Paraserianthes falcata</i> (L.) I. Nielsen	spruce	<i>Picea</i>
parsnip	<i>Pastinaca</i>	stonefruits, apricot, cherry, peach, plum	<i>Prunus</i>
passion fruit	<i>Passiflora</i>	strawberry	<i>Fragaria</i>
pawpaw	<i>Asimina</i>	subalpine fir	<i>Abies lasiocarpa</i> (Hook.) Nutt.
peach	<i>Prunus persica</i> Sieb. & Zucc.	Sudan colanut	<i>Cola acuminata</i> (Pal.) Schott & Endl.
pear, pome fruit	<i>Pyrus</i>	sugar maple	<i>Acer saccharum</i> Marsh.
pecan	<i>Carya illinoensis</i> (Wangenh.) K. Koch	sugarcane	<i>Saccharum officinarum</i> L.
Persian walnut	<i>Juglans regia</i> L.	sunbush	<i>Bossiaea</i>
persimmon	<i>Diospyros</i>	sunbush	<i>Bossiaea laidlawiana</i> Tovey & Morris
pindrow fir	<i>Abies pindrow</i> Royle	swamp mahogany	<i>Eucalyptus robusta</i> Sm.
pine	<i>Pinus</i>	sweet orange	<i>Citrus sinensis</i> Osbeck
pistachio	<i>Pistacia</i>	sweetcane	<i>Saccharum</i>
planetree	<i>Acer pseudoplatanus</i>	sycamore	<i>Platanus occidentalis</i> L.
pomegranite	<i>Punica</i>	sycamore	<i>Platanus</i>
ponderosa pine	<i>Pinus ponderosa</i> Dougl. ex Laws.	tawa	<i>Beilschmiedia tawa</i> (Cunn.) Kirk
poplar	<i>Populus</i>	tawa	<i>Beilschmiedia</i>
potato	<i>Solanum tuberosum</i> L.	tea	<i>Camellia</i>
provence broom	<i>Cytisus purgans</i> (L.) Boiss.	teak	<i>Tectona</i>
quaking aspen	<i>Populus tremuloides</i> Michx.	terminalia	<i>Terminalia</i>
Queensland kauri	<i>Agathis robusta</i> F.M. Bailey	thuja	<i>Thuja</i>
radiata pine	<i>Pinus radiata</i> D. Don	tomato	<i>Lycopersicon</i>
red alder	<i>Alnus rubra</i> Bong.	toon	<i>Toona</i>
red maple	<i>Acer rubrum</i> L.	tung	<i>Aleurites</i>
red oak	<i>Quercus rubra</i> L.	tungoiltree	<i>Aleurites fordii</i> Hemsley
red pine	<i>Pinus resinosa</i> Ait.	turkey oak	<i>Quercus cerris</i> L.
red spruce	<i>Picea rubens</i> Sarg.	walnut	<i>Juglans</i>
rimu	<i>Dacrydium cupressinum</i> Sol. ex Lambert	wandoo	<i>Eucalyptus wandoo</i> Blakely
rose	<i>Rosa</i>	western hemlock	<i>Tsuga heterophylla</i> (Rafn.) Sarg.
rubber tree	<i>Hevea</i>	western larch	<i>Larix occidentalis</i> Nutt.
Sakhalin spruce	<i>Picea glehnii</i> (Schmidt) Mast.	western redcedar	<i>Thuja plicata</i> Donn ex D. Don
sand pine	<i>Pinus clausa</i> (Chapm.) Vasey	western white pine	<i>Pinus monticola</i> Dougl. ex D. Don
scarlet oak	<i>Quercus coccinea</i> Michx.	white fir	<i>Abies concolor</i> (Gord. & Glend.) Lindl. ex Hildebr.
Scots pine	<i>Pinus sylvestris</i> L.	white mulberry	<i>Morus alba</i> L.
senna	<i>Cassia</i>	white oak	<i>Quercus alba</i> L.
sequoia	<i>Sequoiadendron</i>	white spruce	<i>Picea glauca</i> (Moench) Voss
Siberian larch	<i>Larix sibirica</i> Ledeb.	willow	<i>Salix</i>
silver birch	<i>Betula verrucosa</i> Ehrh.		
silver fir	<i>Abies alba</i> Mill.		
silver-beech	<i>Nothofagus menziesii</i> (Hook. f.) Oerst.		

Scientific Names — Common Names

SCIENTIFIC NAMES

<i>Abies</i>	fir, true fir
<i>A. alba</i> Mill.	silver fir
<i>A. balsamea</i> (L.) Miller	balsam fir
<i>A. concolor</i> (Gord. & Glend.) Lindl. ex Hildebr.	white fir
<i>A. grandis</i> (Dougl. ex D. Don) Lindl.	grand fir
<i>A. lasiocarpa</i> (Hook.) Nutt.	subalpine fir
<i>A. pindrow</i> Royle	pindrow fir
<i>Acacia</i>	acacia
<i>A. dealbata</i> Link	silver wattle
<i>A. decurrens</i> (Wendl.) Willd.	green wattle
<i>A. mangium</i> Willd.	brown salwood
<i>Acer</i>	maple
<i>A. pseudoplatanus</i>	planetree
<i>A. rubrum</i> L.	red maple
<i>A. saccharum</i> Marsh.	sugar maple
<i>A. saccharinum</i> L.	silver maple
<i>Actinidia</i>	kiwifruit
<i>Agathis</i>	Agathis
<i>A. australis</i> Salisb.	Queensland kauri
<i>A. robusta</i> F. M. Bailey	kauri
<i>Ailanthus</i>	ailanthus
<i>Albizia</i>	albizia
<i>A. falcata</i> Merr.	albizia
<i>Aleurites</i>	tung
<i>A. fordii</i> Hemsley	tungoiltree
<i>Alnus</i>	alder
<i>A. rubra</i> Bong.	red alder
<i>Araucaria</i>	araucaria
<i>Arundinaria</i>	cane
<i>Asimina</i>	pawpaw
<i>Banksia</i>	banksia
<i>B. grandis</i> Willd.	greatcone banksia
<i>Beilschmiedia</i>	tawa
<i>B. tawa</i> (Cunn.) Kirk	tawa
<i>Beta</i>	beet
<i>Betula</i>	birch
<i>B. papyrifera</i> Marsh.	paper birch
<i>B. verrucosa</i> Ehrh.	silver birch
<i>Bossiaea</i>	sunbush
<i>B. laidlawiana</i> Tovey & Morris	sunbush
<i>Brachystegia</i>	barkclothtree
<i>B. spiciformis</i> Benth.	spike barkclothtree
<i>Callitris</i>	cypress pine
<i>Calocedrus</i>	incense-cedar
<i>C. decurrens</i> (Torr.) Florin (<i>Libocedrus decurrens</i> Torr.)	incense-cedar
<i>Camellia</i>	tea
<i>C. sinensis</i> (L.) Ktze.	common tea
<i>Carica</i>	papaya

SCIENTIFIC NAMES

<i>Carya</i>	hickory
<i>C. illinoensis</i> (Wangenh.) K. Koch	pecan
<i>Cassia</i>	senna
<i>Castanea</i>	chestnut
<i>C. dentata</i> (Marsh.) Borkh.	American chestnut
<i>Casuarina</i>	beefwood
<i>Ceanothus</i>	ceanothus
<i>C. velutinus</i> Dougl.	snowbrush
<i>Cedrela</i>	cedrela
<i>Cedrus</i>	cedar
<i>C. deodora</i> G. Don ex Loud.	deodar
<i>Chamaecyparis</i>	falsecypress
<i>C. obtusa</i> Endl.	hinoki
<i>Cinchona</i>	cinchona
<i>Citrus</i>	citrus
<i>C. aurantifolia</i> (Christmann in L.) Swingle	lime
<i>C. aurantium</i> L.	sour orange
<i>C. sinensis</i> Osbeck	sweet orange
<i>Cocos</i>	coconut
<i>Coffea</i>	coffee
<i>Cola</i>	colanut
<i>C. acuminata</i> (Pal.) Schott & Endl.	Sudan colanut
<i>Corylus</i>	hazelnut
<i>Cryptomeria</i>	cryptomeria
<i>C. japonica</i> (L.) D. Don	Japanese redcedar
<i>Cupressus</i>	cypress
<i>C. lusitanica</i> Mill.	Mexican cypress
<i>Cytisus</i>	broom
<i>C. purgans</i> (L.) Boiss.	provence broom
<i>Dacrydium</i>	dacrydium
<i>D. cupressinum</i> Sol. ex Lambert	rimu
<i>Daucus carota</i> L.	carrot
<i>Diospyros</i>	persimmon
<i>Elaeis</i>	oilpalm
<i>E. guineensis</i>	African oilpalm
<i>Eucalyptus</i>	eucalypt-gum
<i>E. cypellocarpa</i> L. Johnson	mountain grey gum
<i>E. deglupta</i> Blume	New Guinea gum
<i>E. delegatensis</i> R.T. Bak.	alpine ash
<i>E. diversicolor</i> F. Muell.	karri
<i>E. dives</i> Schau.	broad-leaved
<i>E. fastigata</i> Deane & Maid.	peppermint
<i>E. globulus</i> Labill. ssp. <i>bicostata</i> (Maid et al.) Kirkp.	brown barrel
<i>E. grandis</i> Hill ex Maid.	southern blue gum
<i>E. marginata</i> Donn ex Smith	flooded gum
<i>E. obliqua</i> L'Hérit.	jarrah
<i>E. radiata</i> Sieb. ex DC.	messmate
	stringybark
	narrow-leaved
	peppermint

SCIENTIFIC NAMES	COMMON NAMES	SCIENTIFIC NAMES	COMMON NAMES
<i>E. regnans</i> F. Muell.	mountain ash	<i>Nothofagus</i>	southern-beech
<i>E. robusta</i> Sm.	swamp mahogany	<i>N. cunninghamii</i> (Hook. f.)	
<i>E. wandoo</i> Blakely	wandoo	Oerst.	myrtle-beech
<i>Fagus</i>	beech	<i>N. menziesii</i> (Hook. f.) Oerst.	silver-beech
<i>F. grandifolia</i> Ehrh.	American beech	<i>Olea</i>	olive
<i>F. sylvatica</i> L.	common beech	<i>Opuntia</i>	cactus
<i>Ficus</i>	fig	<i>O. ficus-indica</i> Mill.	Indian fig
<i>F. carica</i> L.	common fig	<i>Paraserianthes</i>	paraserianthes
<i>Fragaria</i>	strawberry	<i>P. falcata</i> (L.) I. Nielsen	paraserianthes
<i>Fraxinus</i>	ash	<i>Parinarium</i>	Parinarium
<i>F. excelsior</i> L.	common ash	<i>P. mobola</i> F. Muell. ex Benth.	Muula
<i>Galeola</i>	orchid	<i>Passiflora</i>	passion fruit, granadilla
<i>G. septentrionalis</i> Reichb. f.	orchid		parsnip
<i>Gastrodia</i>	orchid	<i>Pastinaca</i>	geranium
<i>G. elata</i> Bl.	orchid	<i>Pelargonium</i>	fish pelargonium
<i>G. cunninghamii</i> Hook. f.	orchid	<i>P. hortorum</i> Bailey	avocado
<i>Gliricidia</i>	gliricidia	<i>Persea</i>	spruce
<i>Gmelina</i>	gmelina	<i>Picea</i>	Norway spruce
<i>G. arborea</i> L.	gmelina	<i>P. abies</i> (L.) Karst.	Engelmann spruce
<i>Gossypium</i>	cotton	<i>P. engelmanni</i> Parry ex Engelm.	white spruce
<i>Grevillea</i>	grevillea	<i>P. glauca</i> (Moench) Voss	Sakhalin spruce
<i>Hevea</i>	rubber tree	<i>P. glehnii</i> (Schmidt) Mast.	black spruce
<i>Humulus</i>	hops	<i>P. mariana</i> (Mill.) B.S.P.	Morinda spruce
<i>Hydnocarpus</i>	chaulmoogratree	<i>P. morinda</i> Link	red spruce
<i>H. anthelminticus</i> Pierre	common	<i>P. rubens</i> Sarg.	Sitka spruce
	chaulmoogratree	<i>P. sitchensis</i> (Bong.) Carr.	pine
<i>Juglans</i>	walnut	<i>Pinus</i>	Arizona pine
<i>J. regia</i> L.	Persian walnut	<i>P. arizonica</i> Engelm.	jack pine
<i>J. hindsii</i> Jeps. ex Smith	northern California	<i>P. banksiana</i> Lamb.	Caribbean pine
	walnut	<i>P. caribaea</i> Morelet	
<i>Khaya</i>	khaya	<i>P. caribaea</i> var. <i>bahamensis</i>	Bahaman pine
<i>Larix</i>	larch	Barr. ex Golf.	
<i>L. decidua</i> Mill.	European larch	<i>P. caribaea</i> var. <i>hondurensis</i>	Honduran pine
<i>L. leptolepis</i> (Sieb. & Zucc.)		Barr. & Golf.	sand pine
Gord.	Japanese larch	<i>P. clausa</i> (Chapm.) Vasey	lodgepole pine
<i>L. occidentalis</i> Nutt.	western larch	<i>P. contorta</i> Dougl. ex Loud.	slash pine
<i>L. sibirica</i> Ledeb.	Siberian larch	<i>P. elliotii</i> Engelm.	
<i>Lavandula</i>	lavender	<i>P. kesiva</i> Boyle ex Gordon	Khasi pine
<i>Leucaena</i>	leadtree	(<i>P. insularis</i> Endl.)	Korean pine
<i>Libotrya</i>	loquat	<i>P. koraiensis</i> Sieb. & Zucc.	western white pine
<i>Litchi</i>	litchi	<i>P. monticola</i> Dougl. ex D. Don	
<i>Lycopersicon</i>	tomato	<i>P. nigra</i> var. <i>maritima</i> (Ait.)	Corsican pine
<i>Macadamia</i>	macadamia	Melville	Mexican weeping
<i>Malus</i>	apple, pome fruit	<i>P. patula</i> Schiede & Deppe	pine
<i>Mangifera</i>	mango		Maritime pine
<i>Manihot</i>	cassava	<i>P. pinaster</i> Ait.	ponderosa pine
<i>Metasequoia</i>	dawn redwood	<i>P. ponderosa</i> Dougl. ex Laws.	
<i>Metrosideras</i>	iron tree	<i>P. ponderosa</i> var. <i>arizonica</i>	Arizona pine
<i>M. polymorpha</i> (Gaug.) Rock	ohia	(Engelm.) Shaw	radiata pine
<i>Monotropa</i>	Indian pipe	<i>P. radiata</i> D. Don	red pine
<i>M. hypopitys</i> L.	Indian pipe	<i>P. resinosa</i> Ait.	eastern white pine
<i>M. uniflora</i> L.	Indian pipe	<i>P. strobus</i> L.	Scots pine
<i>Morus</i>	mulberry	<i>P. sylvestris</i> L.	loblolly pine
<i>M. alba</i> L.	white mulberry	<i>P. taeda</i> L.	mountain pine
<i>Musa</i>	banana	<i>P. uncinata</i> Mill. ex Mirb.	

SCIENTIFIC NAMES	COMMON NAMES	SCIENTIFIC NAMES	COMMON NAMES
<i>Pistacia</i>	pistachio	<i>Robinia</i>	locust
<i>P. vers</i> L.	common pistachio	<i>Rosa</i>	rose
<i>Platanus</i>	sycamore	<i>Rubus</i>	blackberry,
<i>P. occidentalis</i> L.	sycamore		raspberry
<i>Populus</i>	poplar	<i>R. loganobaccus</i> L. Bailey	loganberry
<i>P. balsamifera</i> L.	balsam poplar	<i>Saccharum</i>	sweetcane
<i>P. grandidentata</i> Michx.	bigtooth aspen	<i>S. officinarum</i> L.	sugarcane
<i>P. tremuloides</i> Michx.	quaking aspen	<i>Salix</i>	willow
<i>Prunus</i>	stonefruits, apricot	<i>S. matsudana</i> Koidz.	Hankow willow
	cherry, peach, plum	<i>Sequoiadendron</i>	sequoia
<i>P. amygdalus</i> Batsch.	almond	<i>Solanum</i>	nightshade
<i>P. armeniaca</i> L.	apricot	<i>S. tuberosum</i> L.	potato
<i>P. cerasus</i> L.	sour cherry	<i>Swietenia</i>	mahogany
<i>P. mahaleb</i> L.	Mahaleb cherry	<i>S. macrophylla</i> King	Honduras
<i>P. persica</i> Sieb. & Zucc.	peach		mahogany
<i>Pseudotsuga</i>	Douglas-fir	<i>Tectona</i>	teak
<i>P. menziesii</i> (Mirb.) Franco	Douglas-fir	<i>T. grandis</i> L. f.	common teak
<i>Psidium</i>	guava	<i>Terminalia</i>	terminalia
<i>Punica</i>	pomegranite	<i>Theobroma</i>	chocolatetree
<i>P. granatum</i> L.	common	<i>T. cacao</i> L.	cacao
	pomegranite	<i>Theobroma</i>	cocoa
<i>Pyrus</i>	pear, pome fruit	<i>Thuja</i>	thuja
<i>Quercus</i>	oak	<i>T. plicata</i> Donn ex D. Don	western redcedar
<i>Q. alba</i> L.	white oak	<i>Toona</i>	toon
<i>Q. cerris</i> L.	turkey oak	<i>Tsuga</i>	hemlock
<i>Q. coccinea</i> Michx.	scarlet oak	<i>T. canadensis</i> (L.) Carr.	eastern hemlock
<i>Q. frainetto</i> Ten.	Hungarian oak	<i>T. heterophylla</i> (Rafn.) Sarg.	western hemlock
<i>Q. pubescens</i> Willd.	downy oak	<i>T. mertensiana</i> (Bong.) Carr.	mountain hemlock
<i>Q. robur</i> L.		<i>Ulmus</i>	elm
(<i>Q. pendunculata</i> Ehrh).	English oak	<i>Vitis</i>	grape
<i>Q. rubra</i> L.	red oak	<i>Widdringtonia</i>	cypress pine
<i>Q. suber</i> L.	cork oak	<i>W. whytei</i> Rendle	mLANJI cedar
<i>Q. velutina</i> Lamarck	black oak	<i>Zizyphus</i>	jujube
<i>Quinine</i>	cinchona		
<i>Ribes</i>	currant, gooseberry		
<i>R. nigrum</i> L.	black currant		

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